Rapid response to abalone virus depletion in western Victoria: information acquisition and reef code assessment

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NON-TECHNICAL SUMMARY

07/066 Rapid response to abalone virus depletion in western Victoria: information acquisition and reef code assessment.

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Objectives:

1. Conduct the scientific surveys at the DPI reef-code sites, using the Victorian survey methods, augmented by genetic sampling and extended survey of the extent of aggregations.
2. Develop a long-term monitoring strategy for continued assessment of reef-stock status and management options.
3. Use existing models to broadly illustrate the likely impacts of the outbreaks.
4. Compile existing information on the outbreaks in an accessible, informative form, develop reef-code growth, maturity and abundance trajectories, and agreed catch histories.
5. Develop and apply a quantitative model that is spatially resolved to the scale of reef-codes, and use this to assess the status of populations and inform the Total Allowable Catch setting process.

Non Technical Summary:

Future management of disease-affected abalone must adapt to the changing circumstances, and adopting a precautionary approach will allow maximum potential for stock recovery. This approach is mandated by the observation that no documented examples are known of abalone populations recovering from catastrophic impacts such as have occurred in the abalone fisheries of Victoria's Western and Central zones. Indeed the balance of international evidence points towards the contrary, so these fisheries are in dangerous territory. This need not mean that recovery cannot occur.

However, the modelling results from this project confirm the above precautionary view and suggest that unless it is known with certainty that disease-induced mortalities have been moderate (less than 40%), then any resumption of fishing in the near term risks the future of the fishery. Acquisition of accurate mortality data is the only basis upon which fishing can recommence in the short term (within 5 years) and in many instances, such as for some among those reefs considered in our study, the opportunity has passed. The simulation results provide guidance, but their validity is conditional on myriad assumptions as well as on the accuracy of data employed. We already know that catches early in the fishery's history were higher than reported officially, but how much higher is conjecture. Growth is highly variable over small spatial scales and feedback effects from reduced abundance together with changed size structure and persistence of habitat will play roles in determining the rate, if any, of recovery. The extent of the contemporary illegal catch is uncertain, particularly given the unprecedented closure of the fisheries. The results show that even small illegal catches can significantly degrade recovery where the viral impact is high, with clear implications for the enforcement aspects of managing these fisheries.

Design of future data collection strategies within Victoria and its neighbouring states of South Australia, New South Wales and Tasmania should be focused on acquisition of base line data and a preparedness to sample disease affected populations as the disease is occurring and subsequently at a frequency that identifies its persistence. For instance, counting and measuring dying and dead abalone and evacuated shells may prove invaluable. Surveys such as these are expensive and industry should consider how it might contribute to the provision of comprehensive geographically detailed data such as size structure and abundance that will be responsive to mortality. Commercial abalone divers, driven by an imperative to earn a living, are already making assertions that the resource has recovered sufficiently to resume harvesting. Our study shows that they may be "telling it like it appears", but that appearances in this instance are deceptive.

Victoria now has a basis for assessing post-disease management complemented by a comprehensive bank of tissue samples ready for testing previous exposure to disease once a properly validated test becomes available and aggregation data for the Western Zone that can be used to discriminate between future changes in true abundance and changes in distribution patterns on reefs due to movements. More work is required to investigate suitable indices that can be calculated from the aggregation data collected to measure changes in patterns over time. Once a reliable genetic test to determine previous disease exposure has been applied, the results should form part of an epidemiological study to ascertain the likelihood of disease recurrence and whether or not future outbreaks are likely to become less lethal.

OUTCOMES ACHIEVED

This project provided survey and other information to support assessment of individual reef-codes in Victoria's Western Zones, and basic models to assess population status and examine management options for these reef-codes. Thus the immediate outcomes were better-informed abalone industry stakeholders in Victoria's Western Zone, the Victorian management agency and Victoria more generally.

However, as this was the first project to build reef-code level assessment models, and the first to design surveys to assess the impact of the new disease on reef stocks it has provided a basis for design and testing of models for reef-scale management of stocks elsewhere, and a tested template for the information that will be required when/if the virus spreads to other regions. Thus the industry generally, and all abalone producing states have benefited.

Keywords: abalone, catastrophic, disease, recovery, modelling

Acknowledgements

The Western Abalone Divers Association (WADA) of the Victorian abalone fishery and the Victorian Department of Primary Industries (DPI) supported this project.

The background text below was adapted from a meeting report authored by Prof. M.G. Chapman, Professor of Marine Ecology, University of Sydney. Prof. Chapman was engaged by WADA to chair a meeting among abalone experts at Port Fairy on 10th – 12th December 2007. WADA hosted the meeting to obtain advice on the advantages and implications of different approaches for post-disease stock recovery.

Special mention must be made of the efforts of contract research diver David Forbes who applied his 25 years experience as a scientific diver to devise a practical and efficient method for conducting aggregation surveys and of Justin Bell, Matt Koopman, Fabian Trinne who against the odds managed to strategically collect genetic samples from more than 150 reef codes.

FINAL REPORT

07/066 Rapid response to abalone virus depletion in western Victoria: information acquisition and reef code assessment

Background

The Victorian abalone fishery, located along the southeastern coastline of the Australian mainland, contributes significantly to the global abalone catch (Gordon and Cook 2001). Active management of the fishery via size-limits and quotas has prevented the collapse seen in other major abalone fisheries. A viral outbreak of a type previously unknown in this region has, however, caused extreme abalone mortality along a 280-kilometre section of the coastline during the past two years and the viral front continues to advance (Fig. 1). The herpes-like virus that causes this lethal disease, called Abalone Viral Ganglioneuritis (AVG), probably entered the coastal waters from a shore-based abalone farming facility, although the origin of the disease prior to this is not known. Since that time, it has spread east and west, bringing nearly all commercial harvesting in the Western Zone to a halt and moving into the Central Zone. It is having major impacts on the viability of the fishery, with possible but as yet unmeasured effects on the ecology of the reefs.

Nevertheless, despite nearly total mortality of adult abalone in many areas of many reefs, mortality is not 100 % everywhere. Some reefs and some patches of impacted reefs appear to have suffered no (or very little) mortality. The reasons for this are unknown. Although it is possible that the remaining abalone are resistant to the virus, it is generally believed that surviving abalone were probably not exposed to the virus. The virus is so virulent that, under laboratory conditions, healthy abalone placed in contact with infected or dead abalone succumb and die within a few days. The high rate of mortality in the field was visible by the abundance of dead and dying abalone and the large number of recent shells. Because juvenile abalone typically occupy cryptic habitat, there are no records of mortality of juveniles, but it is assumed to be similar to that of adults. Indeed, it may be greater because the cryptic habitat used by juveniles (e.g. crevices, underneath boulders, etc.) may be more likely to bring animals into close proximity and enhance spread of the disease.

Surprisingly, considering the time since the outbreak and the major implications on the viability of the commercial fishery, there is not yet a test to determine whether (i) remaining abalone have been exposed to the virus and are resistant, (ii) other species carry the virus, nor (iii) whether affected reefs still have evidence of the virus persisting.

Once a PCR test has been developed (still a matter of months) and the Western Zone surveyed for signs of the virus, three options are available. First, if there are still persistent signs of the virus, decisions will have to be made about continued fishing of the remaining stock, taking into account viability of the species, the fishery and the spread of the virus.

Since the resulting population state is well outside historical bounds, previous responses to fishing pressure are not useful indicators of likely recovery. Furthermore, the high spatial variability of viral mortality necessitates reef-scale management of the post-viral fishery. Accordingly a simulation approach is warranted, with model parameters estimated against reef-scale data and simulated recovery scenarios informed by mortality estimates at the reef level. Robust guidance to fisheries managers faced with unprecedented decisions about when and under what circumstances to re-open closed areas following the passage of disease is imperative. Economic imperatives are driving many commercial abalone divers to apply substantial pressure to re-open the fishery as soon as possible amidst claims of "stock recovery" and "low disease impact". Absence of persuasive quantitative information to the contrary will make it difficult for managers to resist this pressure when attempting to make objective decisions that will promote medium to longer-term sustainability.

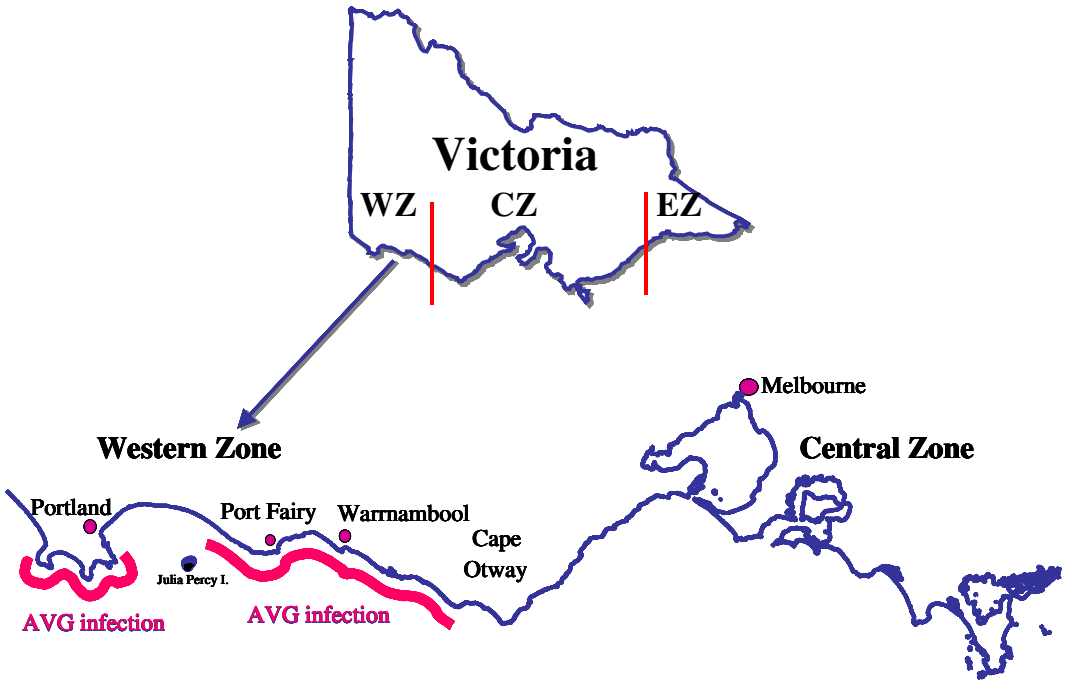

Figure 1. Map of Victoria's western and central coasts showing the abalone fishery management zone boundaries and illustrating the disease-affected region considered in this study.

Need

The Western Abalone Divers Association arranged a workshop on 25–26 June 2007 to review available information about the virus outbreaks from previous reports, commercial diver observations, dive observations by Dr Jeremy Prince and scientific surveys by the Victorian Department of Primary Industries, and determine the implications for monitoring, stock assessment and management advice. The workshop was chaired by Dr Keith Sainsbury and included leading abalone scientists from Victoria and South Australia. This workshop initiated the project proposal, thus industry supported it from inception as well as becoming involved in its delivery. The proposal also received the support of Fisheries Victoria (FV), the relevant management agency.

The workshop review concluded that (1) there were significant gaps and limitations in the existing information on the status of the abalone populations across reefs in western Victoria (West and Central zones) and exposure of these populations to the virus and (2) that FV's regional model was inadequate to represent the current situation in the western zone or to evaluate management options.

In relation to information needs, it was concluded that there was an urgent need to repeat scientific surveys at all the standard monitoring sites in the Western Zone, and far enough into the Central Zone to be ahead of the virus outbreaks, during July-August 2007. It was also decided that the standard sampling for fishery independent abundance should be augmented by genetic sampling and a broad survey of aggregations among the reefs.

The regional quantitative model was inadequate for representing the current situation in the Western Zone or to evaluate alternative management options. This was because the current situation in the Western Zone involved a form of depletion that was very different from the effects of fishing, in terms of the size classes affected and extent of depletion. Reefs were affected differentially and the management options were also likely to vary by reef, but the existing regional model could not represent reefs in its existing form. Because the current situation was unique, there was no longer a basis for assuming that the previously-used industry-based semi-quantitative assessment of reef codes would continue to be reliable.

Thus there was clearly a need to develop and apply a quantitative model that could be spatially resolved to at least the reef-code level, and to use this for assessment of population status and examination of management options at the reef-code level.

Objectives

Information acquistion

1. **Conduct the scientific surveys at the DPI reef-code sites, using the Victorian survey methods, augmented by genetic sampling and extended survey of the extent of aggregations.**
2. **Develop a long-term monitoring strategy for continued assessment of reef-stock status and management options.**

Reefcode assessment

3. **Use existing models to broadly illustrate the likely impacts of the outbreaks.**
4. **Compile existing information on the outbreaks in an accessible, informative form, develop reef-code growth, maturity and abundance trajectories, and agreed catch histories.**
5. **Develop and apply a quantitative model that is spatially resolved to the scale of reef-codes, and use this to assess the status of populations and inform the Total Allowable Catch setting process.**

Methods

Data acqusition

Surveys of reef-code sites

Surveys were conducted at 38 fixed survey sites established by MaFFRI and surveyed annually during the previous 17 years. The surveys used the standard MaFFRI methodology (Gorfine et al. 1998), but were augmented by genetic sampling and extended surveys of the extent of aggregations. The numbers, patch sizes and spacing among aggregations were estimated from 150 belt transects 80 m long by 1 m wide between 6 Sep and 28 Nov 2007. Length frequency measurements were also obtained to determine population size structure. Details of the sampling protocol are provided in Appendix 3.

Long-term monitoring strategy

These surveys were used to establish a basis for continued assessment of stock status and management options. Discussion was held about designing an industry-based assessment process that will also draw upon work conducted by SARDI in the Southern Zone of the South Australian abalone fishery. This strategy will make greater use of commercial divers than the current methodology funded by Fisheries Victoria.

Genetic (PCR) sampling

Samples comprising tissues taken from 10 individual abalone from each of about 100 sites were collected from the majority of reef codes throughout Victoria during 2007. There were several instances where only 5 samples taken while repeat sampling selected sites. Seven of the samples were from sites with evidence of recent infection, one during active disease and 21 from locations where previous infection had been confirmed by histopathological testing. Greenlip abalone samples were also taken from various locations and several additional blacklip abalone samples were collected from non-commercial reefs along the coast between Lorne and Point Lonsdale. These were locations where recreational diving activity is prevalent. Ten sites were sampled in Port Phillip Bay.

The sampling protocol involved aseptic removal of tissue from the cephalic region and subsequent freezing. A sterile scalpel blade was used to make cuts 1 cm either side of the buccal cavity extending towards the posterior about one quarter of the length the foot to remove a block of tissue about 2cm wide and 3cm long from each abalone. Each block of tissue was then transferred into a labelled plastic vial and immersed in liquid nitrogen. Sample vials were subsequently transported to the laboratory where they were transferred into a freezer set at –80°C. These samples are now stored at DPI's Queenscliff and Attwood laboratories awaiting completion of the development of a reliable PCR test.

Reefcode assessment

Illustrative modelling

Existing models were used to inform both government and industry about the broad situation in the short-term, ahead of a more definitive assessment from a more definitive reef-code model that could not be built and tested within a time-frame that met the TACC setting timetable for the 2008–09 quota year. Possible scenarios using the current national abalone model to illustrate impact and recovery scenarios for a range of population types (e.g. more or less productive), pre-outbreak stock status (e.g. level of depletion), intensities of outbreak mortality, and harvesting strategy were produced. In addition, the Abasim interactive fishery management software was refined into a version that provided a more flexible package tailored to the Western Zone that allowed user-friendly exploration of the impacts and recovery of reefs under different management options.

Compilation of existing information

Information on the timing and geographic extent of the outbreaks was summarised from Victoria's DPI and industry sources, and compiled in an accessible and informative form to provide useful information to modellers, managers, and industry stakeholders. Reef-code growth, maturity and abundance trajectories were developed from existing datasets. Mortalities were estimated from pre-and post disease abundance surveys. Historical catch trends (with and without notional illegal and unreported catches) for each reef-code and population length-frequency and standardised fishery independent abundance time series were used to fit the quantitative model.

Reef-code level quantitative model

A model was developed from the national abalone model that could be used to represent all reef-codes individually. Specifications for this model included:

- Common natural mortality across reef codes.
- Reef code specific maturity and growth derived from the current semi-quantitative classification of reef-codes based on shell characteristics.
- A stock-recruitment relationship with a common steepness across all reefs, but a reef-specific asymptote.
- Historical catch data as the major model input and scientific survey data for fitting the generated biomass trajectories for the different industry reef codes. Relative weighting among indices of abundance was be explored to derive optimal fits in each instance.
- Consider different levels of viral impact assuming no instances of recurrence.
- Examine various hypotheses about the dynamics of recovery, including possible ecosystem effects that result in deterioration of abalone habitat quality.
- Evaluate possible management measures, especially catch levels, but potentially including size limit change, translocation of healthy mature abalone and fish-down on reefs ahead of the outbreaks.
- Integrate with a user-friendly, graphical display. Consider using the revised Abasim software for this purpose.

This project delivered the samples and model to allow reef-code stock assessment and evaluation of management options in the future. The methodology was based on the assumption that other research and management activities would be required to enable full use to be made of the outputs from this project. In particular it was assumed that there will be:

- research to develop definitive genetic tests for the presence and previous exposure of abalone to the virus, and that these tests would be applied to the abalone samples collected by the current project;
- research to develop hypotheses about the dynamics of transfer, infection and mortality due to the AVG virus, and that these hypotheses will be incorporated into future versions of the reef-scale population model developed by the current project;
- resources available, through the usual TACC setting process or through newly dedicated processes, to allow application of the model developed through this project to assess the status of abalone populations and to evaluate alternative management options for quota years beyond 2008–09.

Specific technical details of the modelling methodology employed are provided in the draft manuscript in Appendix 3.

Results/Discussion

Among the five components of the project the major emphasis is on the fifth with the other four mostly providing the means to developing the reef code level quantitative model.

Data acqusition

A number of the components initiated will not yield results for some time, but nevertheless this project has established an important baseline for future assessment. Principally these include sampling for genetic testing to establish previous exposure to AVG among apparently healthy or surviving abalone populations and initial surveys of aggregations. There were no pre-disease aggregation data for statistical comparison. Abalone samples from most reef codes throughout

Victoria (about 150) were collected for future PCR testing during annually surveys of fixed monitoring sites. This should provide an assessment of the extent of previous exposure to AVG for the entire state once a reliable PCR becomes available. It is unclear at present when this will eventuate. Follow-up aggregation surveys will be required as a back-up measure in the event that abundance appears to have recovered. The data collected during this project will enable discrimination between re-aggregation among existing abalone and real increases in overall abundance.

Surveys of reef-code sites

Only simple statistical summaries of the fishery independent abundance and aggregation surveys (based on exploratory data analysis) are presented in this report. More complex spatial statistics for the aggregation data were beyond the resources of the project and could more appropriately applied and evaluated within the context of a follow-up survey pending availability of the necessary research funds to support such work. The routine annual abundance survey data have been used in the reef-code level quantitative model.

Fishery independent abundance surveys

Trends in abundance standardised for time series ending for each of the past three years clearly illustrate the overall impact of disease related mortalities in the Western Zone since (Fig. 2). Note that the years in the graph representing the year in which the preceding quota year commenced so that 2006 is the 2006–07 quota year with abundance surveys completed during 2007. This is necessary because the modelling operates on an annual time-step so that catches are assumed to have been taking prior to each abundance survey.

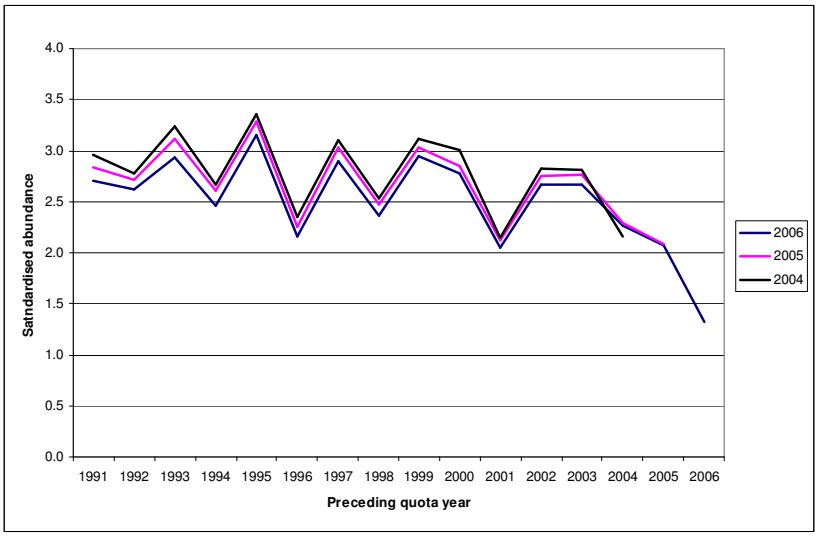

Figure 2. Standardised fishery independent abalone abundance showing pre- and post-disease trends across all emergent size-classes and all locations in the Western Zone of the Victorian abalone fishery.

When abundance data prior to the disease outbreak are considered separately for the Portland and Port Fairy regions it is evident that Portland's populations had experienced a period of generalised decline, whereas the Port Fairy populations were apparently stable (Fig. 3).

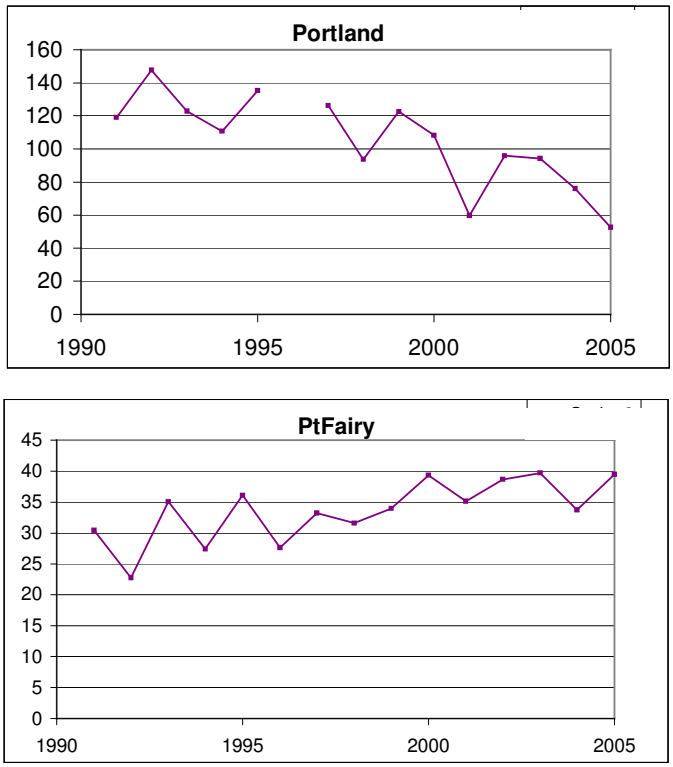

Figure 3. Standardised trends in fishery independent abalone abundance for Portland and Port Fairy regions prior to the outbreak of AVG among wild blacklip abalone populations at Port Fairy during May 2006.

Aggregation surveys

Numbers of aggregations per transect among reef codes varied substantially, ranging from two to 26 (Table 1). Median patch sizes among reef codes varied from one to five abalone and median spaces between patches ranged from 2.1 to 9.0 m (Table 1). Frequency distributions of both patch sizes (Fig 4) and intervals (Fig 5) were skewed to the right with many solitary abalone at least 30 cm, but less than several metres, apart and most patches containing up to 8 abalone. At the other extreme was a patch containing 212 abalone in reef code 1.02 (Whites Beach) and two patches spaced 61.2 m apart in the one 80 m transect at reef code 1.05 (Cape Bridgewater).

Although direct comparison of future surveys could be made using the same statistic as presented be here, there are a wide range of integrated measures of dispersion and patchiness used by ecologists and natural resource scientists that may be useful in the study of abalone aggregations. Selection of an appropriate measure would require extensive comparisons and careful consideration about he underlying statistical assumptions and applicability to our data. Such an evaluation is beyond the resources of this tactical project but would be a worthwhile scientific endeavour. The design of the aggregation sampling was pragmatic, taking into consideration those limitations imposed by the need to make large numbers of reliable quantitative estimates when underwater in often hostile sea conditions. Inevitably, this leads to a requirement to develop a *post-hoc* approach to analysing data.

Table 1. Summary statistics from transect-based aggregation surveys for individual reef codes in the Western Zone of the Victorian abalone fishery during Sep – Nov 2007.

Reef code	Reef names	Transects	Total patches	Patches per transect	Median size (no./patch)	Median patch spacing (m)
1.02	Whites	8	93	12	5	2.1
1.03	Petrified Forest, Southwest Bridgewater, Watersprings	12	106	9	3	3.0
1.05	Cape Bridgewater, Pebble Beach	12	97	8	3	2.8
1.07	Seal Caves, Horseshoe	8	15	2	2	8.0
1.08	Horseshoe	4	8	2	1	9.0
2.01	Murrells inshore	4	66	17	2	3.1
2.02	Murrells offshore	4	105	26	2	2.8
2.04	Cape Nelson, Nelson Cave, Washing Machine Rock	12	70	6	2	4.0
2.05	Killer Waves Kill Reef	4	63	16	2	3.2
2.06	Inside Cape Nelson	4	63	16	1	5.1
2.09	The Passage	4	8	2	3	6.1
3.02	Northwest Lady Julia Percy I.	4	61	15	3	3.2
3.03	Lady Julia Percy Island	4	30	8	3	4.5
3.04	Propellor Bay Centre & East - Lady Julia Percy I.	8	152	19	4	2.1
3.05	The Crags	20	236	12	3	3.4
3.08	Port Fairy Lighthouse	8	26	3	2	4.7
3.09	Mills Reef	8	116	15	2	2.0
3.10	Killarney	6	65	11	2	3.1
3.11	Levys & The Cutting	12	48	4	2	6.3

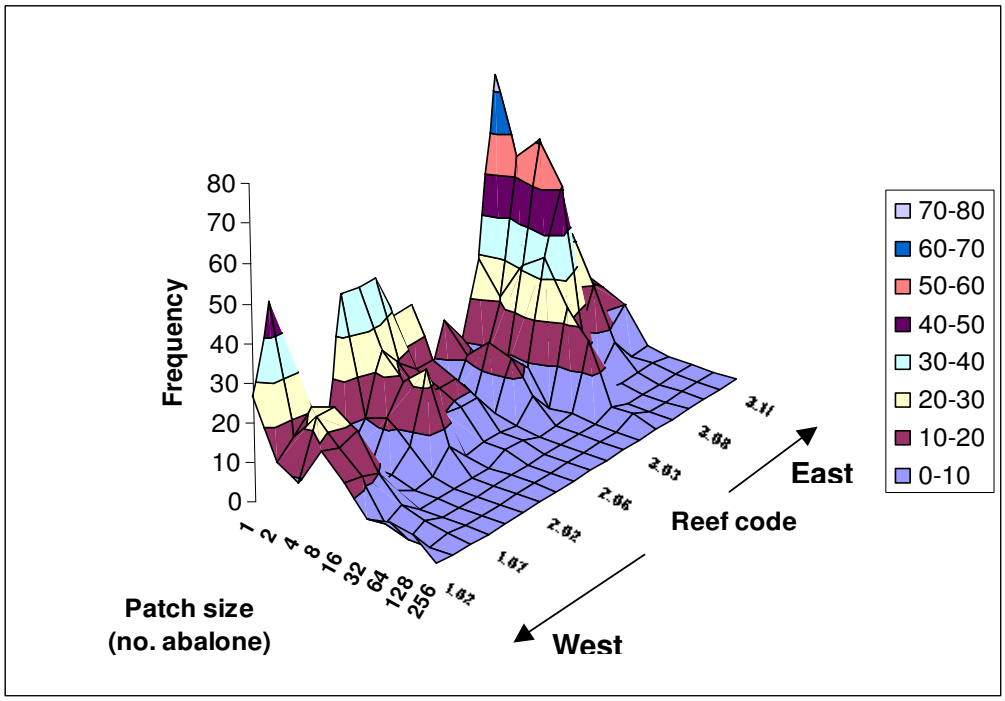

Figure 4. Distribution of different patch sizes of blacklip abalone for individual reef codes in sequence along the coast in the Western Zone of the Victorian abalone fishery during Sep – Nov 2007.

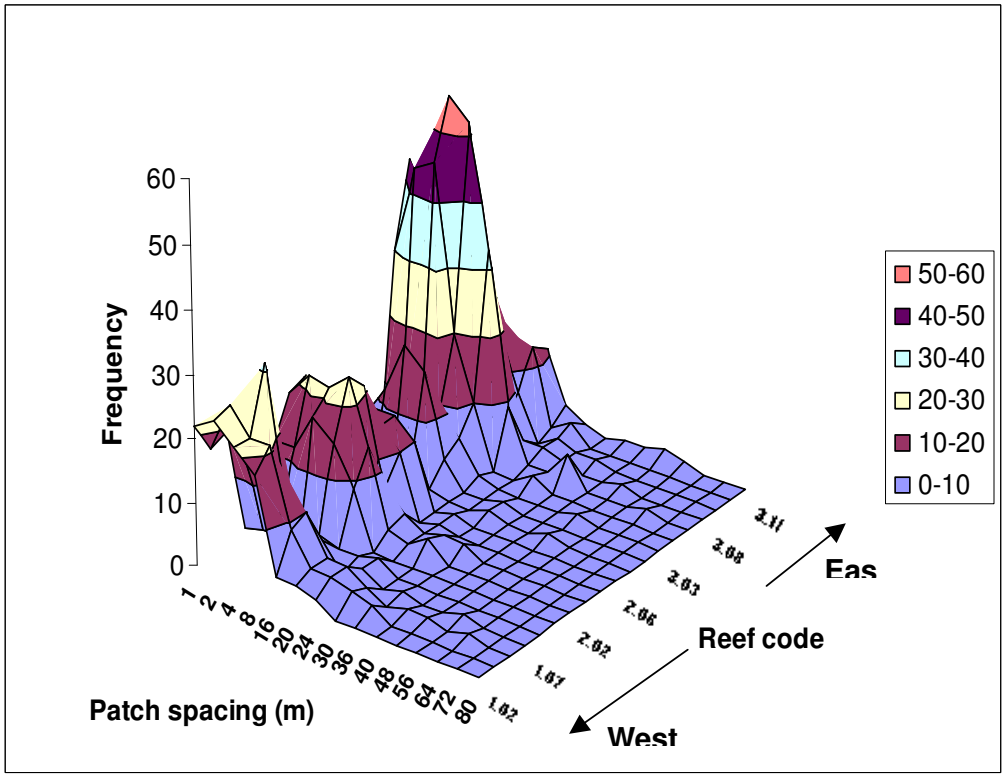

Figure 5. Distribution of distances among blacklip abalone patches for individual reef codes in sequence along the coast in the Western Zone of the Victorian abalone fishery during Sep – Nov 2007.

Long-term monitoring strategy

A long-term industry based monitoring strategy of affected and unaffected reefs in the Western Zone has been planned, however development of the methodology was beyond the time constraints and resources available to this project. Consequently a strategic meeting of abalone scientists was held by WADA at The University if Melbourne on 27–28 June 2008 to discuss alternative methods and develop a strategy. This strategy has since formed the basis for drafting a separate TRF funding proposal to FRDC to support the development of an industry based sampling and survey methodology to monitor the recovery of AVG afflicted abalone stocks. This project is intended to calibrate abalone diver surveys with existing state government funded fishery independent surveys and to provide appropriate training for commercial abalone divers. A project implementation meeting is scheduled to coincide with the 4th National Abalone Convention at Port Lincoln during September 17–19 2008 pending a successful outcome for the application.

Reefcode assessment

Illustrative modelling

Two independent approaches were adopted for illustrative modelling as described in the Methods. Results from these separate research activities were presented on the 11 Dec 2007 at Port Fairy. Results from the national model based approach were presented in static format although based on stochastic modelling. These depicted the effects of likely AVG mortalities on the size structure and recovery potential of key reefs within the zone. The amount and quality of data underpinning each modelled reef code varied, affecting the reliability of the results. Nonetheless, outputs demonstrated that recovery would most take many years for most reefs. The results also showed that substantial benefits could accrue from using a very conservative size limit if harvesting was to continue in the shorter term.

The modelling based on Abasim was deterministic, however the software enabled a dynamic presentation that provide and more informative engagement of industry members in discussion about possible post-disease scenario. There was reasonable congruency between both modelling approaches providing reassurance that the outputs were reasonable given the necessary assumptions and data limitations. However, it is must be stressed that outputs from Abasim will only be generally indicative and may bear little resemblance to the real life outcomes of such a patchily distributed species, whose dynamics are so driven by size rather than age.

Reef-code level quantitative model

Results from the quantitative modelling for individual reef codes is presented comprehensively in the draft manuscript in Appendix 3. The following is an extract from the discussion of results in the manuscript.

The processes that lead to the numbers and size composition of abalone that become visible to divers as the stocks recover are likely to be heavily masked by the pattern of emergence of abalone from cryptic habitat. Thus we focus first on the numbers of all the mature size-classes, before and after the disease impact. The simulation for reef code 3.05, one of the first productive

areas hit by AVG, if the mortality were 80% is shown in Figures 6 and 7. In general the reefs had all reached a fairly stable equilibrium between harvesting of larger adults and recruitment to larger sizes, prior to the disease impact. This balance is characterised by relatively low proportions of the largest size classes (>130 mm). On many reefs the voluntary increases in harvest size limits between 2002 and 2007 had increased numbers of 130–140 mm and larger abalone (black, purple). As fecundity increases roughly with the cube of length, and thus in proportion to biomass, the numbers of these larger abalone are most important in determining the how many recruits grow into the modelled stock each year. If smaller adults increase growth rather than fecundity when density is reduced, as Dixon and Day (2004) suggest for greenlip

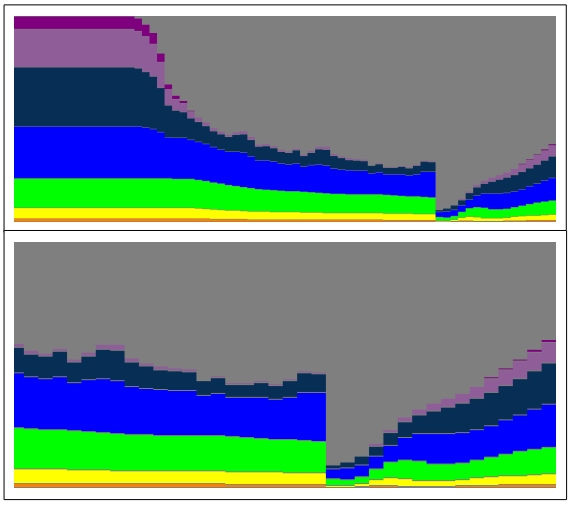

Figure 6. Baseline scenario for reef code 3.05 with 80% viral mortality. Relative abundance is presented in 10mm size classes for clarity (the model uses 2mm classes for all calculations). Emerged abundance provides a "diver's eye view" of the population, but the total abundance provides a more biologically meaningful picture.

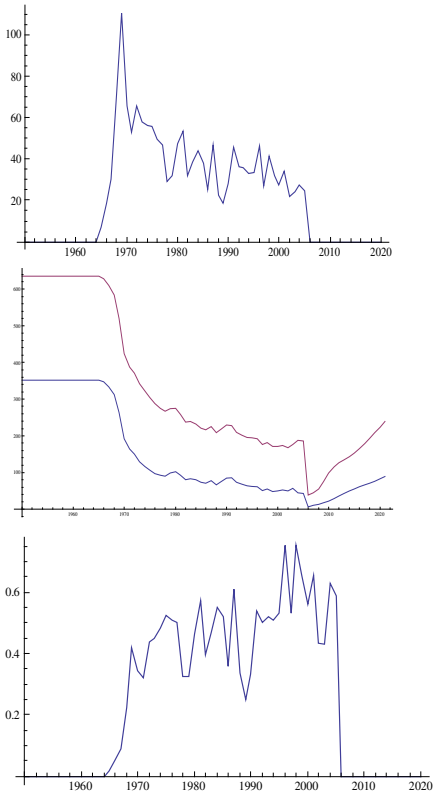

Figure 7. Key biomass trajectories derived during the baseline scenario for reef code 3.05 with 80% viral mortality.

abalone, then larger abalone would influence recruitment even more strongly at low population densities.

As the model considers abalone >52 mm and juvenile growth is variable, the recruitment each year into the modelled stock depends on juveniles produced in 3 previous years, so that recruitment is related to a weighted sum of total adult biomass in each of the 3 prior years. This, together with variable growth of abalone in the modelled size classes smoothes the changes in recruitment to mature sizes over time.

As we assume the virus impacts all sizes equally, both the modelled stocks and the recruitment of juveniles from previous years is reduced after the disease impact. A 30% stock reduction (Figure 8) leads to fairly rapid subsequent exponential increases in adult stocks, partly because growth of the remaining larger adults rapidly increases total fecundity, and partly because the stock-recruitment function dictates there will be more recruits per unit mature biomass at low density. The growth rate of larger abalone slows, so that abalone accumulate faster in the 130–140 and >140 mm size classes than for smaller sizes, and they are not removed as the reefs remain closed to fishing (in these simulations). Thus the numbers of these two largest size classes exceed the pre-virus numbers within 2 years, even though the total numbers of mature abalone do not recover until 7 years after the disease impact. This effect, plus the fact that the divers see mostly only the size classes over 110 mm, in which most are not cryptic, means that the recovery appears to be much faster (4 years) in the diver's eye view of the reef (Figure 8),

Note that the model does not take into account any density-dependent growth, nor any decrease in the size at emergence from crevices once substantial numbers of emergent adults die, nor any effects of aggregation of remaining abalone into the best habitat patches, where commercial divers will focus their search. These three mechanisms would all increase the apparent abundance of abalone on reefs to commercial divers, and all probably occur to some extent (Dixon and Day 2004, McAvaney et al. 2004, Officer et al. 2001), but we have insufficient data to estimate such effects and thus incorporate them into our model.

If the disease removes 80% of each size-class (Figure 6), then the growth of the reduced numbers of juveniles and smaller adults adds to the numbers >130 mm more slowly, but with the same pattern, so that numbers of these large adults reach pre-virus levels after 8 years, while the total numbers of adults recover to pre-virus levels only after about 20 years. The diver's eye view however, would suggest that the stocks had recovered to 2000 levels after 17 years (Figure 8).

The reefs modelled differ in the abundance and size-distribution of abalone present before the disease impact, as well as in growth rates. Thus the number of years required to ensure a high probability of recovery varies between reefs (Figure 9). Reef area 3.10, for example, recovers more rapidly than other areas. But these differences are small in comparison to the effect of the mortality rate that the disease inflicts on a reef. This emphasizes the importance of accurate measurement of these mortality rates as the disease spreads further into the Central Zone, or perhaps in other areas. The only means to do this appears to be surveys prior to, and soon after the disease event on each reef area.

The simulations of each reef are informed by estimates of catch histories, and one of the largest uncertainties is the degree of illegal catch in each area in the past. If the reef stocks sustained larger catches in the past than we have estimated, then the stock reduction by the virus is a smaller percentage of the total reduction of the virgin biomass since the fishery began. Thus one might expect less compensatory response in recruitment to the disease reduction, as is shown for reef codes 3.10 and 3.11 in Tables 4 and 5, where the illegal or unreported catch is assumed substantially higher than the reported catch.

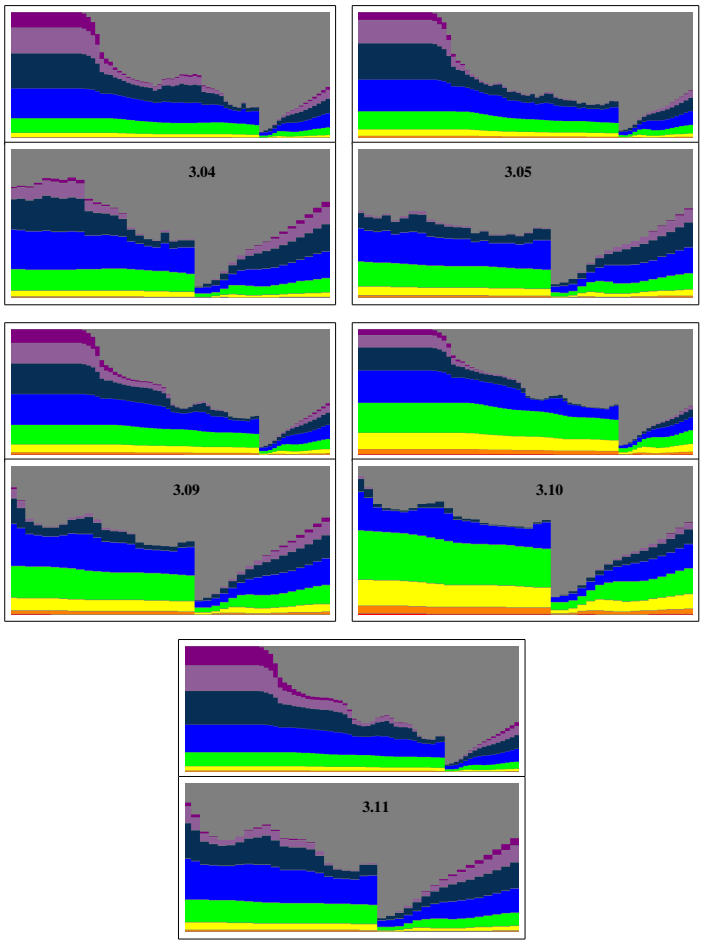

Figure 8. Emerged and total abundance, in 10mm size classes, for a range of viral impacts applied to the baseline scenario for reef code 3.05.

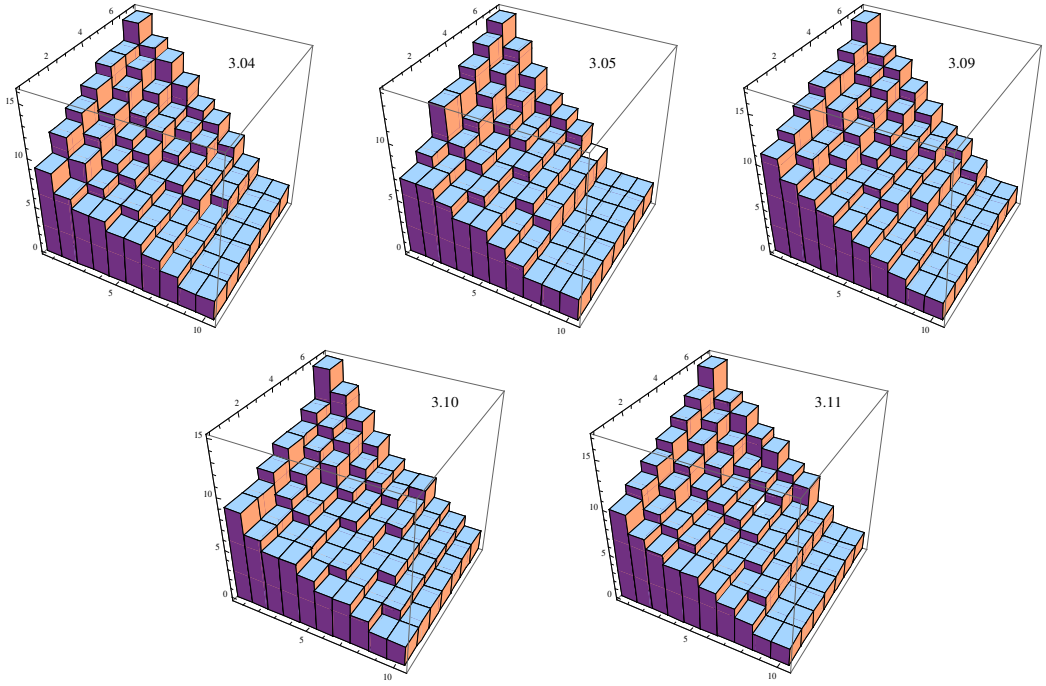

Figure 9. For each of the five Port Fairy reef codes studied, the effect of recruitment fluctuations on recovery is illustrated by plotting recovery times as a function of viral impact % and probability of recovery.

Benefits

This project provided survey and other information to support assessment of individual reef-codes in Victoria's Western and Central zones, and basic models to assess population status and examine management options for these reef-codes. Thus the immediate beneficiaries were the abalone industry stakeholders in Victoria's western and central zones, the Victorian management agency and Victoria more generally.

This was the first project to build reef-code level assessment models, and the first to design surveys to assess the impact of the new disease on reef stocks. Thus this work provided a basis for design and testing of models for reef-scale management of stocks elsewhere, and a tested template for the information that will be required when/if the virus spreads to other regions. Thus the industry generally, and all abalone producing states have benefited.

Further Development

Future management of disease-affected abalone must adapt to the changing circumstances, and adopting a precautionary approach will allow maximum potential for stock recovery. This approach is mandated by the observation that no documented examples are known of abalone

populations recovering from catastrophic impacts such as have occurred in the abalone fisheries of Victoria's Western and Central zones. Indeed the balance of international evidence points towards the contrary, so these fisheries are in dangerous territory. This need not mean that recovery cannot occur.

However, the modelling results presented here confirm the above precautionary view and suggest that unless it is known with certainty that disease-induced mortalities have been moderate (less than 40%), then any resumption of fishing in the near term risks the future of the fishery. Acquisition of accurate mortality data is the only basis upon which fishing can recommence in the short term (within 5 years) and in many instances, such as for some among those reefs considered in our study, the opportunity has passed. The simulation results provide guidance, but their validity is conditional on myriad assumptions as well as on the accuracy of data employed. We already know that catches early in the fisheries' history were higher than those reported officially, but how much higher remains conjecture (one of the authors is aware of the existence of cash sales books for the early years of the fishery that were confiscated by Australian Federal Police about fifteen years ago, however the current location of these valuable documents remains a mystery). Growth is highly variable over small spatial scales and density dependence effects together with size structure and persistence of habitat will play roles in determining the rate, if any, of recovery. The extent of the contemporary illegal catch is uncertain, particularly given the unprecedented closure of the fisheries. The results given here show that even small illegal catches can significantly degrade recovery where the viral impact is high, with clear implications for the enforcement aspects of managing these fisheries.

Design of future data collection strategies within Victoria and its neighbouring states of South Australia, New South Wales and Tasmania (despite its separation from the mainland by Bass Strait) should be focused on acquisition of base line data and a preparedness to sample disease affected populations as the disease is occurring and subsequently at a frequency that identifies its persistence. For instance, enumeration and measurement of morbid and dead abalone and evacuated shells may prove invaluable. Surveys such as these are expensive and industry should consider how it might contribute to the provision of comprehensive spatially resolved data such as size structure and abundance that will be responsive to mortality. Commercial abalone divers, driven by an imperative to earn a living, are already making assertions that the resource has recovered sufficiently to resume harvesting. Our study shows that they may be "telling it like it appears", but that appearances in this instance are deceptive.

Planned Outcomes

The anticipated outcomes from the application of outputs from this project were better informed stakeholders in the Western Zone of the Victorian abalone fishery faced with TACC decisions in the wake of catastrophic, but variable, disease-induced mortalities and better prepared stakeholders among those abalone fisheries that have not been afflicted as yet but may experience outbreaks of AVG in the future.

The model outputs clearly illustrated that recovery is likely to be slow, that divers' perceptions although genuine do not necessarily provide a true picture of the severity of the impact and that a most precautionary approach to future management is warranted. WADA and Fisheries Victoria have responded with a level of conservatism in setting TACCs and LMLs for 2008–09 commensurate with the results from this project and are strategically planning how to intensively monitor recovery at the reef scale. Industry-based monitoring will build on the modelling that was developed and baseline aggregation data that was collected during this study, as intended, augmented by additional observations related to spawning levels and shell morphology and morphometrics that build on existing work from FRDC funded projects at SARDI and The University of Melbourne.

The modelling and aggregation surveys can provide guidance about the kinds of baseline sampling and assessment strategies that those abalone fisheries unaffected by AVG should now consider to better enable them to cope in the event that their fisheries become afflicted. More beneficial outcomes will accrue in this regard after genetic testing of the samples collected during this study has been done that should provide more enlightenment about the way AVG is spread and whether re-infection of a population is likely following additional expose to the virus.

Conclusion

In summary the key points are:

- Stock recovery is likely to take more than one generation.
- Larger abalone influence recruitment even more strongly at low population densities.
- Effects of spatial differences in size structure and growth rate are small compared with the disease induced mortality rate. This emphasizes the importance of accurate measurement of these mortality rates.
- Expect less compensatory response in recruitment to the disease reduction, as is shown for reef code 3.05 (The Crags), where the illegal or unreported catch is assumed to be 1.5 times the reported catch.
- Absence of recurrence is a necessary precondition to the validity of the model outputs.

References

Dixon, C.D. & R.W. Day. 2004. Growth responses in emergent greenlip abalone to density reductions and translocations. Journal of Shellfish Research. 23: 1223–1228.

Gordon, R. & P.A. Cook. 2001 World abalone supply, markets and pricing: Historical, current and future, Journal of Shellfish Research. 20: 567–570.

Gorfine, H.K., D.A. Forbes & A.S. Gason. 1998. A comparison of two underwater census methods for estimating the abundance of the commercially important blacklip abalone, Haliotis rubra. Fishery Bulletin 96: 438–450.

McAvaney, L.A., R.W. Day, C.D. Dixon & S.M. Huchette. 2004. Gonad development in seeded Haliotis laevigata: growth environment determines initial reproductive investment. Journal of Shellfish Research 23: 1213–1218.

Officer, R. A., H. K. Gorfine & C. D. Dixon. 2001. Movement and re-aggregation of the blacklip abalone, Haliotis rubra, after fishing. Journal of Shellfish Research. 20: 771–779.

Appendix 1: Intellectual Property

The reef-code models incorporated IP (information) belonging to WADA, Jeremy Prince, and DPI. The design of the software was based on the National abalone model, developed by MaFFRI with FRDC funding, and incorporated design IP from D. Bardos, C. Dichmont and K. Sainsbury.

Appendix 2: Staff

Harry Gorfine and Rob Day led the project, however no staff were directly employed on this project. Instead, consultants D. Bardos, C. Dichmont, J. Prince and K. Sainsbury were engaged to advise, complete and review the modelling components and Aquatic Research Support Services (ARSS) was hired to conduct underwater aggregation surveys. ARSS did not charge for the collection of the PCR samples during their routine surveys.

Appendix 3:

Field survey protocol SOP:

ARSS (Principal: David Forbes)
STANDARD OPERATING PROCEDURE
Sep-Nov 2007 Abalone Surveys
West of Port Campbell MNP

24 Hours Prior to Work.

- Contact Fisheries Victoria on (03) 9483 4283 and leave the following message:

Prior notification, possible abalone research <…location….> , <date of work day(s) Permit number RP_____, <…name……>, <mobile number…>

Eg. Prior notification, possible abalone research, Port Fairy, Sunday to Wednesday Permit number RP525, David Forbes 0407316088.

MORNING of EACH WORK DAY

- Contact Fisheries Victoria on (03) 9483 4283 and leave the following message:

Abalone research <…location….> Permit number RP_____, <…name……>, <mobile number…>

Eg. Confirmation, abalone research, Port Fairy, today, Permit number RP525, David Forbes 0407316088.

AT EACH SITE

- GPS locations and site numbers, are as per normal annual surveys.
- Gear to be deployed at each site:
    - Centre weight and two swim lines, with six catch bags attached.
    - Each diver to take a "data board" and tape measure, a watch on a clip, and an abalone iron
- Aggregation surveys are to be completed first.
- Aggregation surveys are to be completed by one diver at 0° and 180° and by the second diver at 90° and 270°.
- After the completion of the Aggregation Surveys, the normal Abundance Survey is to be completed.

Underwater Method

- Once at the bottom, divers will clip their tape measure to the central weight, find their pre determined compass direction and begin collecting data immediately, i.e. zero meters is the weight.
- The transect for these data will be as per the normal survey method, that is the tape will be run from the divers left side and the transect will be one metre to the right of this point.
- Every abalone encountered in this one meter wide transect will be considered the start of an aggregation. Record the distance from the weight to this abalone in decimetres i.e. 25.3m (twenty five point three meters)
- Every abalone within 30cm of this first individual will be considered to be part of the same aggregation. This includes abalone that continue outside the normal transect in either direction.
- An abalone more than 30cm from it's nearest neighbour will be considered to be the start of a separate aggregation, which if it falls inside the normal one meter transect (or is connected by abalone within 30cm of each other to one that does fall inside the normal transect) will be recorded as part of the next aggregation.
- The exact number of individuals in each aggregation is to be recorded. (So the record an aggregation would appear as i.e. 25.3m / 64)
- Sand Patches wider than 3mtrs will be recorded as the distance at which they begin and then the distance at which they end. (ie 25.5m start sand, 33.2m end sand) .
- Recording of Aggregation data will occur until the first of the following occurs:
    - The distance of 80 m from the central weight is achieved.
    - The shoreline / cliff face is encountered
    - The depth has been consistently deeper than 18m for at least 10m distance.

- At the completion of the first 80m (max) long transect, the diver rewinds the tape back to the central weight, re-sets their compass for the reciprocal direction and begins their second swim as above.
- Once both 80m (max) Aggregation surveys have been completed the diver then completes their three pre-assigned Abundance survey transect **as per normal**, including the recording of all environmental, geological, geographical, habitat, floral and faunal information and the counting and grading of all abalone encountered. A collection of 25 abalone, timed to

minutes and seconds must also be collected at the end of each transect. RANDOM Directions for Abundance surveys to have 10° add to them to provide clearance between two survey methods. NB in the early years we added 10° every year so this is not a new concept

- Once both aggregation surveys and three abundance surveys, including length frequency collections have been completed, prepare to send all gear to the surface. Replace all returned abalone and exit the water.

On Deck.

At each site ensure that the following are completed:

Deckhand / Standby Diver

As well as all duties associated with the safety of the vessel and the divers, including hose maintenance.

- Log divers into water.
- Prepare data sheets
- Record time when Red Button is pushed.
- Data Log every abalone that is sent up.
- Record first abalone information.
- Return measured abalone (non sample) to the bottom.
- Record last abalone information.
- Log divers out of water.
- Retrieve all gear and put into detergent soaks.
- Record time when Green Button is pushed

Divers

Once back on deck:

- Transpose data for 3 normal transects and complete normal data sheet
- Transpose Aggregation Data onto data sheet
- Clean all data boards of information
- Disinfect and prepare for departure.

BACK AT THE BOAT RAMP

- Contact Fisheries on (03) 9483 4283 ASAP and leave the following message:

Post diving report, landing <boat ramp>, Permit number RP_____, <…name……>, <mobile number…>

Eg. Post diving report, landing Port Fairy, Permit number RP525, David Forbes 0407316088.

- Ensure that a full decontamination takes place EVERY NIGHT.
- Remove data logger for charging
- Remove completed data sheets.
- At the end of each run the DataSafe (blue box) should be removed from logger and returned with data to MaFFRI. An emptied DataSafe will be given to you for the next trip.

Draft manuscript:

Reef-scale abalone population dynamics: recovery from a high-mortality viral event.

D. C. Bardos, H. K. Gorfine, B. Taylor and R. W. Day

Reef-scale abalone population dynamics: recovery from a high-mortality viral event.

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Abstract

The Victorian fishery for blacklip abalone (*Haliotis rubra* Leach 1814), located along the southeastern coastline of the Australian mainland, contributes significantly to global abalone catches. Active management of the fishery via size-limits and quotas has prevented collapses seen in other major abalone fisheries. A recent viral outbreak of a type previously unknown in this region has, however, caused extreme abalone mortality along an extensive section of coastline and the viral front continues to advance. Because the disease affects all size classes and those abalone inhabiting cryptic spaces inaccessible to divers, previous population responses to excessive fishing mortality of legal-sized accessible abalone are not useful as predictors of the likely time frame and extent of recovery. Furthermore, the high spatial variability of viral mortality necessitates reef-scale management of the post-viral fishery. Accordingly a simulation approach is being extensively employed, with model parameters estimated against reef-scale data and simulated recovery scenarios informed by mortality estimates at the reef level. Here we present estimation and simulation results for five reefs of particular importance in post-viral management of the fishery. These results are critical in providing guidance to fisheries managers faced with unprecedented decisions about when and under what circumstances to re-open closed areas following the passage of disease. Economic imperatives are driving many commercial abalone divers to apply substantial pressure to re-open the fishery as soon as possible amidst claims of "stock recovery" and "low disease impact". Absence of persuasive quantitative information to the contrary will make it difficult for managers to resist this pressure when attempting to make objective decisions that will promote medium to longer-term sustainability.

1. Introduction

Abalone are gastropod molluscs, of cultural significance in much of Asia as a delicacy served at restaurants and during ceremonial events such as weddings (Hahn 1989). Large species of abalone are found in most cool temperate coastal region (Geiger 2000, Lindberg 1992), and the advent of compressed air diving equipment resulted in a rapid rise in exploitation rates after World War II. Global abalone production was estimated to be around 25,000 tonnes at its zenith during the mid 1970s (Gordon 2001), but wild fisheries production has since declined substantially, succumbing variously to habitat change, disease and especially over-exploitation, often via illegal fishing (Shepherd et al. 1992b). A burgeoning aquaculture industry has replaced much previous wild production, but aquaculture has been beset with its own problems of production and economic viability, especially those stemming from disease (Cook

1998, de Waal & Cook 2001, McBride 1998, Simizu & Uchino 2004, Wang et al. 2004, Zhang et al. 2004).

Indeed, the contemporary abalone story has been one of progressive, often dramatic collapse of populations and their associated fisheries, initially in the earlier-established fisheries of the Northern Hemisphere (Gordon 2001, see also Shepherd et al. 1992b), and more recently among the remaining viable fisheries of the Southern Hemisphere (Tarr 1995). Averting further collapses appears an elusive goal despite the persuasive lessons from history and a receptive community of scientists and stakeholders eager to learn from the past.

Population biology

We are fortunate in that more is known about the biology of abalone than almost any other fish stocks, especially in Australia (Day & Shepherd 1995). Abalone are relatively long-lived molluscs, with adults exhibiting low rates of natural mortality and high fecundity (McShane 1995). For instance, a tagged greenlip abalone (*Haliotis laevigata*) was recovered 20 years after release (Shepherd pers. comm.). This is counter-balanced by high natural mortality rates during juvenile life stages (McShane 1991). Recruitment of postlarval abalone to reefs tends to be episodic and of variable density (McShane 1995), but density dependent mortality and growth (Huchette et al 2003; Day et al. 2004) would smooth recruitment to larger sizes. Growth is highly variable over small spatial scales (Troynikov and Gorfine 1998), as is spawning (McShane 1995). Abalone maturity appears to be largely age related (Nash 1992), and size at maturity is highly variable between populations (Prince 2003, 2005, Shepherd et al. 1992a). Although abalone begin producing small numbers of ripe eggs while still growing rapidly (McAvaney et al. 2004), growth slows considerably as the gonad enlarges to produce millions of eggs (Day & Fleming 1992). Fecundity (number of eggs) is linearly related to biomass and shell volume (Shepherd et al. 1992a). Abalone are broadcast spawners with separate sexes, so fertilisation takes place in the water column and reductions in local adult density are likely to exponentially decrease the probability of fertilisation (Babcock and Keesing 1999), although this may be offset by aggregative behaviour (Officer et al. 2001). Larval supply is mostly localised (Prince et al 1987, 1988, McShane et al. 1998), but with potential for occasional dispersal over large distances under suitable circumstances, giving rise to a large genetic neighbourhood size but spatially limited recruitment (Hancock 2000).

Large abalone appear to have few natural predators. Heterodontid sharks and rays appear to be their main predators, and Blacklip abalone typically comprise about 25% of the gut contents of Port Jackson sharks in south-eastern Australia (T. Walker unpub. data). Large seastars consume abalone only in unusual circumstances (Day et al. 1995). Smaller sizes however, are eaten by wrasses, octopus, lobsters and crabs (Shepherd & Godoy 1989). Presumably as a result, many abalone species occupy cryptic spaces that offer protection from predation when small, and some proportion emerge as they grow larger and mature. This presents a substantial problem for accurate underwater visual census to survey populations (Gorfine et al. 1998).

Surveys of abalone abundance are carried out using underwater census (Gorfine et al. 1998), however despite our best efforts to survey abalone populations within transects at fixed sites, abundance data are characteristically variable due to the patchy distribution of abalone and localised movement dynamics (McShane 1995a.).

Although net displacements are generally small, movements occur in response to anthropogenic, predatory and environmental disturbances. At micro-scales abalone are typically found clustered together in locations where food delivery by water movement is more prolific. However, when disturbed by predators abalone will move away from their homesites. Those removed by human predators will often, but not always, be replaced by others presumably seeking prime locations to inhabit.

Although many abalone fisheries have suffered catastrophic declines, Australian abalone fisheries have hitherto escaped. In 2006 however, massive mortalities of wild abalone began in the Western Zone of the commercial abalone fishery in Victoria, as a result of a virus that attacks abalone nerve ganglia (Hooper et al. 2007), and is thus called abalone viral ganglioneuritis (AVG). Since that time, the disease has spread widely to encompass about 280 km of coastline, bringing much commercial harvesting in the Western Zone to a halt in 2008. The disease however, spread slowly and in a concentrated front, and has not returned to previously infected reefs, so that those Western Zone reefs that were affected in 2006 have had some time to recover.

Reefs in the Port Fairy region were generally considered stable prior to the disease outbreak, however the abundance patterns clearly show that for some reefs this perception was not necessarily well founded. The Western Zone abalone industry had progressively increased size limits of a voluntary basis during recent years and the benefits were starting to show in terms of slowing or reversal of declining abundance (Prince et al 2008) up until they became affected by disease. It is not known to what extent this has reduced the disease impact and will aid future recovery, but variation in pre-disease stock status will undoubtedly have some influence.

The high mortality due to this virus and its apparent uniformity across the age-size structure results in a depletion of the fishery well outside historical experience, where even the heaviest fishing mortality occurred only in non-cryptic adult size-classes. Consequently it is impossible to rely directly on previous recoveries from fishing depletion as a guide to post-viral recovery. Instead, the previous history of the fishery is used to estimate parameters in a reef-scale model of abalone population dynamics, which is then applied to generate recovery trajectories under various viral-mortality assumptions.

The fishery

The Victorian abalone fishery commenced during the early 1960s and reported commercial catches rapidly rose to about 3000 tonnes during the ensuing decade. Illegal fishing for high value commercial species such as abalone is inevitable and there is strong anecdotal evidence that substantial amounts of unreported catch were taken during the developing years of the Victorian abalone fishery prior to the introduction of catch quotas (Gorfine et al. 2002, McShane 1990). Unregistered cash sales of catches were a common occurrence among those intent on avoiding tax obligations. Catch quotas totalling 1440 tonnes were introduced during 1988 to stabilise the fishery and secure its future sustainability. A comprehensive fishery independent population-monitoring program was initiated soon afterwards that has continued to the present. Population modelling commenced during the late 1990s following almost a decade of monitoring. As the vast majority of the catch is blacklip abalone (*Haliotis rubra* Leach 1884) all modelling has been developed for this species. A stochastic length-based model was developed that uses catches as principal inputs and fits outputs of estimated biomass to trends in abundance (Gorfine et al. 2005). Management by the state is now based on annual quotas for three management zones (Eastern, Central and Western) that each span several hundred kilometres of coastline (Fig. 1), and Legal Minimum Lengths (LMLs) that apply across broad areas (Fisheries Victoria 2002).

As with the majority of contemporary fisheries models, maximum likelihood estimation is supplanted by a Bayesian methodology. Although the model could be applied to individual populations, data limitations mean that it has only been run at relatively large spatial scales, encompassing many populations. Modelled biomass is used as a performance measure, with specific reference points linked to the annual quota decisions for each zone (Fisheries Victoria 2002).

The fact that local stocks are separate and vary in size at maturity means that LMLs applied regionally may protect all the breeding abalone in locations with a small size of maturity, but allow total removal of breeding stock in productive areas with larger sizes of maturity (Prince 2003, 2005). Further, zonal TACs encourage focused fishing effort in preferred diving areas – often productive areas where all the emergent abalone will be above the LML, so that harvesting is fast. State financial resources however, are - and under cost recovery in each state will remain - insufficient to support assessment and management of individual reef-stocks (Prince et al. 2008).

Beginning in 2002, all three of the zonal industry organisations have collaborated with the Victoria Department of Primary Industries (DPI) to develop fine scale management of the resource, based on commercial diver assessments of the size at which abalone become fully mature on each reef (Fig. 2), and the size distribution of abalone catches (Prince et al. 2008). The associations have increased voluntary size limits above the legal minimum length and set agreed catch caps on reefs at collaborative workshops based on such data, to protect more vulnerable stocks by providing a more balanced distribution of catches among reefs. These initiatives had substantially improved previously declining stocks on many reefs (Prince et al. 2008).

Consequently, there has been a shift from relying solely on government regulated zone-scale management based on the model to augmenting this with industry-driven reef scale voluntary assessment and management. Catch quotas in the all zones have

been progressively reduced during recent years in response to both modelled biomass estimates and industry assessments of sustainable catch aggregates based on the estimated productive potential of stocks on individual reefs.

Disease outbreak

The first outbreak of AVG among wild abalone in the Western Zone during May 2006 followed mass mortalities from the same disease in a land-based abalone farm that discharges effluent into the sea nearby (Appleford 2007). The effects of this virulent disease on nerve tissue causes abalone to lose pedal adhesion and detach from the rock, and predators then rapidly devour dying and dead abalone. During these mortality events substantial quantities of possibly infectious mucous and tissue fragments become suspended in the water, and this may disperse the virus towards uninfected populations. Mortalities were highly variable among populations within the study area (Fig. 3), and differences between pre and post disease fishery independent abundance surveys were variably influenced by pre-disease harvesting (Fig. 3).

AVG has now spread unabated in both westerly and easterly directions during the two years since the initial outbreak, to infect almost all abalone populations over 300 km of coastline, without any apparent reduction in virulence. The affected area currently encompasses most reefs in western Victoria, from west of Cape Otway in the Central Zone to Discovery Bay in the Western Zone (Fig. 2). There are now only a few unaffected regions, such as Lady Julia Percy Island (Fig. 2), and one plausible explanation for their disease-free status is that these are geographically isolated from other abalone habitat.

Although confirmed cases of AVG infection were detected sequentially from west to east throughout the study region the timing of fulminant disease is only known circumstantially. For example, a single diseased abalone was found at Mills Reef during July 2006, however this was an isolated case and AVG had not fully to encompassed the entire region from The Crags to The Cutting until January 2007 (Fig. 2). This makes it difficult to associate declines in abundance with onset of disease with any precision. Complicating matters further at Mills and Killarney, abundance on the sites on the outer reef perimeter increased after disease was initially detected whereas those on the inner areas were consistent with the timing of disease onset. Some industry observers have speculated that the disease affected abalone populations worst in instances where there was some protection from the incident ocean swell and reduced flushing out to seawards. This implies that infectious material suspended in the water column inside barrier reefs had remained in contact with abalone for longer periods increasing the chance of infection. Once disease was established within the inner reef populations then it is possible that this led to subsequent infection of the more exposed populations on the outer reef areas 2–3 months later. It is important to emphasised that whilst plausible this is conjecture and that an alternative explanation may exist.

Reefs were progressively closed to fishing as AVG spread. The disease persists in an area from weeks to months and it is presently unknown if re-infection can occur, although no subsequent outbreaks have been seen in previously diseased populations. TACCS were reduced in proportion to the catch histories of the closed areas. In the Western Zone, holders of 14 fishery access licences had to share a TACC of 16 tonnes

of blacklip and 4.2 tonnes of greenlip abalone, plus nominal allocations totalling another 42 tonnes of catch issued under exploratory permits, during 2008–09; accessed from only four (of 38) reef code areas that remained disease-free. This was a 72% reduction from the TACC of 221 tonnes set in 2005/6 prior to the initial viral outbreak. In the Central Zone a TACC of 462 tonnes of blacklip and 3.4 tonnes of greenlip has been allocated among 34 licences, compared with a previous TACC of 680 tonnes. It is important to note that TACCs had been decreased and size limits increased on reefs to avert or redress stock declines, with some signs of success, prior to the AVG outbreak.

The extraordinary mortalities have severe implications for future sustainable harvests levels in the Western and Central zones. Critically, the sizes of clean shells washed ashore near reefs suggests all size classes are similarly affected by AVG. Losses among sub-legal sized abalone will compromise stock recruitment in the near future and may depress population recruitment over the longer term. Significant fecundity (millions of gametes) probably occurs only after 5 years as growth slows, so that loss of juveniles and pre-recruits as well as adults means it may be many years before sufficient recruitment occurs to replenish stocks. Although when previously unexploited stocks are fished, compensatory density dependence may lead to increased productivity (reproductive output, survival and growth), the relationship between stock and recruitment may well become depensatory at very low adult densities. One hypothesis is that larger abalone on reefs maintain the corallines on which abalone larvae settle (Morse et al. 1979, Shepherd and Daume 1996).

It is impossible to separate mortalities due to disease from other sources by estimating changes in the numbers of living abalone. Indeed, the quota reductions in the Western and Central Zones relate partly to over-harvesting prior to the disease (Prince et al. 2008). However, there were no indications of diseased abalone in the wild when fishery independent abundance surveys were conducted in the Western Zone during late February 2006 (Appleford **2007**). During subsequent surveys on disease-affected reefs in 2006, observations of atypical morbidity and mortality combined with large numbers of recently evacuated shells were compelling indicators that disease was the main cause of reduced abundance. It is rare to observe large numbers of empty abalone shells. Rough seas generally cause abalone shells to disintegrate rapidly, so that high shell numbers point towards recent rather than cumulative mortality events. Most previous observations of clusters of empty shells have been associated with illegal fishing, involving removal of the flesh underwater.

Regardless of source, the impact of mortalities on abundance must be accommodated when setting a TACC for the following quota year (1 April to 31 March). Our conventional modelling at regional scales was clearly unsuited to the new circumstances, so an alternative approach was sought. The key question was when could reefs be considered to have recovered? We applied a simulation model at the scale of individual reef complexes to predict the probable time for recovery for several key reefs in the Western Zone. Recovery was defined as when 90% of the relative biomass in the year 2000 (the specified reference point in the Victorian Abalone Fishery management Plan) was attained. The main challenge was to deal with a lack of precise information about disease-induced mortality rates for each reef, especially among cryptic abalone, and changes in post-viral size structure among legal sized survivors that had grown large in the absence of fishing. When commercial

abalone divers inspected abalone populations on several reefs, both factors may have led many into believing that these populations had recovered. However, divers cannot see the hidden impact on those cryptic and mostly smaller animals in the disease-affected populations. What they observed were simply the effects of growth and movement. This is because the time frame since the disease had abated was too short for any net increase in numbers of abalone to become apparent from recruits to these populations. The modelling undertaken in this study attempted to address this problem of hidden impact on population recruitment and subsequent stock recovery. The objective was to illustrate likely time frames before resumption of harvesting could be considered under different scenarios.

Methods

3. Reef-scale modelling approach

Assessment of the fishery, prior to the disease outbreak, included the development of a zonal-scale fishery model (Gorfine et. al. 2005), incorporating size-structured, discrete-time population dynamics regulated by a Beverton-Holt stock-recruitment relation. Additional population structure was included in the form of cryptic and emerged subpopulations and an associated size-dependent emergence profile. This model is driven by annual catch and size-limit data and estimated against length-frequency and relative-abundance time-series via Bayesian analysis, using Markov-Chain Monte Carlo (MCMC) methods. Typically an annual time-step is employed and size classes are 2mm in width, from 52mm to 162mm. In broad terms, the population dynamics structure and parameter estimation methods used in the model lie within the standard practice (Quinn and Deriso, 1999) of contemporary fisheries stock assessment modelling.

The zonal-scale model aggregates data from many distinct abalone populations that, whilst essentially localized to a reef-scale, have previously been managed primarily at the zonal level. However, since the viral impact is observed to be highly spatially variable, it is necessary to manage recovery at a reef-scale. Accordingly, the zonal model has been adapted for estimation from reef-scale data and for post-viral recovery simulation at a reef-scale. Details of the particular variant of this model employed in the present work are given below.

3.1 Data acquisition

Commercial catch

Commercial catch landings were recorded since the late 1960s, however reef-coding systems have changed several times during this period and it was difficult to verify catches at current reef-code reporting scales prior to 1979. Some recent length frequency data from sampling the commercial catch were also available, but observations varied among reefs and years. The accuracy of commercial catch has improved substantially since the introduction of quotas in 1988 and more recently during the current decade following the introduction of a comprehensive audit trail of documentation supported by electronic data acquisition. Contemporary catches are weighed on certified calibrated scales at the point of landing and catch weights for

each reef code fished are now reported in real time via an integrated voice response (IVR) system accessed by mobile telephone. Abalone divers' deckhands measured length-frequency of catches on an ad hoc basis whilst at sea using purpose-built shellfish-measuring machines coupled electronically to data loggers.

Population abundance

Time series of fishery independent abundance and length frequency were acquired via underwater surveys conducted annually during 1992–2009. At each fixed monitoring site, initially selected haphazardly on commercially productive reefs, abalone were either collected (pre-Year 2000) or counted (2000 onwards) by research divers from within belt transects 30 m long by 1 m wide.

Initially, 18 fixed sites were established throughout most of the commercial abalone fishing grounds in the Western Zone. Depths of sites were constrained to between 4–18 metres to minimise divers' exposure to excessive surge and hyperbaric exposure respectively. Site numbers were progressively increased over the years to 38, providing a more comprehensive coverage of the fishing grounds. Site numbers were increased in conjunction with a reduction in within site replicate transects, from the original nine per site to six from Year 200 onwards. This followed exploratory statistical analysis that showed that in most instances the precision for six transects per site was less than 0.25. The number of sites surveyed for the reefs in this modelling study ranged from five at The Crags to two at each of Mills and Killarney.

In general, divers were randomly assigned three transects each for each site, although there were instances where 4–5 transects were completed by one diver for logistical or safety reasons. Where counts were undertaken instead of collections (at least the last half of the time series), 25 additional abalone were collected at the conclusion of each transect to provide a pool of 150 abalone per site, numbers permitting, for measuring length-frequency. Transects from "non-normal" divers (mean transect collections from comparative exercises differed significantly from standard divers or SE/mean > 0.25) were excluded from analyses. Data were standardized using a Generalised Linear Model (Genmod procedure in SAS) with diver, site and season as the independent (predictor) variables and abundance as the dependent (response) variable.

3.2 Population dynamics

This model allows for movement into and out of cryptic habitat and for fishing size-selectivity to vary between years. Recruitment to the model is assumed to be restricted to the cryptic habitat. The number of abalone in length-class l at time $t+1$ is determined by applying growth, natural mortality, fishing mortality (catch) and recruitment to the number of abalone in each length-class $l' < l$ via the equations

$$N^{c}_{t,l} = \alpha_l \left(\sum_{l' \le l} N^{c}_{t\text{-}1,l'} e^{-M^{c}_{l'}} [1 - \sum_{i} F^{i}_{t\text{-}1} S^{i}_{t\text{-}1,l'}] X^{c}_{l,l'} + \sum_{l' \le l} N^{\tilde{c}}_{t\text{-}1,l'} e^{-M^{\tilde{c}}_{l'}} X^{\tilde{c}}_{l,l'} \right) \qquad (1a)$$

$$N^{\tilde{c}}_{t,l} = (1-\alpha_l)(\sum_{l'\le l} N^{c}_{t\text{-}1,l'} e^{-M^{c}_{l'}}[1-\sum_i F^{i}_{t\text{-}1} S^{i}_{t\text{-}1,l'}]X^{c}_{l,l'} + \sum_{l'\le l} N^{\tilde{c}}_{t\text{-}1,l'} e^{-M^{\tilde{c}}_{l'}} X^{\tilde{c}}_{l,l'}) + R_{t\text{-}1,l} \qquad (1b)$$

where $N^{c}_{t,l}$ is the number of abalone in size-class l in non-cryptic habitat at the start of year t,

$N^{\tilde{c}}_{t,l}$ is the number of abalone in size-class l in cryptic habitat at the start of year t,

α_l is the probability that an animal in size-class l is in the non-cryptic habitat (the emergence ogive).

$M^{c/\tilde{c}}_{l}$ is the instantaneous rate of natural mortality on animals in size-class l in the non-cryptic / cryptic habitat,

$X^{c/\tilde{c}}_{l,l'}$ is the probability that an animal in the non-cryptic / cryptic habitat and size-class l' grows into size-class l in a single year (the size-transition matrix),

F_t is the fully-selected commercial exploitation rate during year t,

$S_{t,l}$ is the fishing selectivity on animals in size-class l during year t, and

$R_{t,l}$ is the recruitment to size-class l at the end of year t.

For the present purposes, emerged and cryptic growth are assumed equal, so that $\mathbf{X}^{c} = \mathbf{X}^{\tilde{c}} \equiv \mathbf{X}$ and similarly we assume $M^{\tilde{c}}_{l} = M^{c}_{l} \equiv M_l$.

Growth

Size-transition (i.e. growth) matrices are derived from fitting a probabilistic Gompertz model (Bardos, 2005) against an extensive set of tag-recapture growth datasets for the region. After the fitting process (which occurs outside the fishery model), the Gompertz model parameters are fixed and only a time-at-liberty parameter Δt needs to be specified in order to generate the transition matrix. Since the population dynamics model employs an annual time-step, we use $\Delta t = 1\text{Yr}$.

However, due to strong spatial variability in abalone growth (Troynikov & Gorfine 1998) and uncertain effects of the tagging process on growth (Day & Fleming 1992), it cannot be assumed that the resulting growth matrix accurately represents growth for a particular reef. In order to allow for further tuning of growth against the abundance and length frequency data from individual reefs, we allow the time-at-liberty used in generating the growth matrices to be multiplied by a parameter, denoted $\delta_{\Delta t}$, which is estimated within the fishery model.

To avoid large computational burdens from repeatedly deriving these matrices (and many arrays depending on them) within lengthy MCMC runs, we restrict $\delta_{\Delta t}$ to a discrete set of 60 values and all resulting arrays required for the population dynamics are pre-calculated in an initial phase prior to the MCMC run.

Catch

Annual commercial catch data (in weight) is assumed to be available, denoted C_t for the commercial catch at the end of year *t*. Additionally, assumptions must be made about the Illegal, Unreported and Unregulated (IUU) catch. Here we consider two scenarios for the IUU catch over the history of the fishery, expressed as a scaling factor ρ_t to be applied to the commercial catch (see Fig. 4), so that the total catch in year t is then $\rho_t C_t$.

The fully-selected exploitation rate appearing in Eq. (1) is defined as the ratio of the total catch to the exploitable biomass, subject to an upper bound of 1 to ensure non-negative numbers in the fished size-classes:

$$\begin{aligned} F_t &= \max\left(\frac{\rho_t C_t}{B_t^{\mathrm{e}}}, 1 \right), \\ B_t^{\mathrm{e}} &= \sum_l w_l \, S_{t,l} \, N_{t,l}^c \, e^{-M_l^c \Delta t}, \end{aligned} \tag{2}$$

where B_t^{e} is the exploitable biomass during year *t* and $w_l = a\, l^b$ is the mean weight of an animal in size-class l, where a, b are the parameters of the weight-size relationship. For weight in kg and length in mm, we use $a = 10^{-7}$ kg mm^{-3}, $b = 3.08$ (see McShane et al. 1988b).

Fishing selectivity

Fishing selectivity as a function of size-class is given by a "knife-edge" function

$$S_{t,l} = \begin{cases} 0, & l < l_t^{\min} \\ \dfrac{p + (1-p)(l - l_t^{\min})}{(l_t^{\max} - l_t^{\min})}, & l_t^{\min} > l > l_t^{\max} \\ 1, & l \geq l_t^{\max} \end{cases} \tag{3}$$

and $l_t^{\min}$ is the minimum length fished for during year *t,*

$l_t^{\max}$ is the first length fully fished during year *t,*

p is the proportion of animals selected at $l_t^{\min}$ during year *t,* so that $S_{t,l}$ reduces to a step function when $p = 1$.

Here we use $p = 0.75$, $l_t^{\max} = l_t^{\min} + 4$ and a time series for $l_t^{\min}$ is derived from legal size limits and (more recently) from voluntary minimum lengths (VMLs) introduced by industry during the past five years.

Transition from cryptic to non-cryptic habitat

Emergence as a function of size-class, is specified as:

$$\alpha_l = (1 + \exp(-\ln(19)(l - l_{50})/\phi))^{-1} \quad (4)$$

where ϕ and l_{50} are the centre and width parameters of the resulting emergence, which is

used (see Eq. 1) to redistribute the animals at each length at the end of each year. It is assumed that emergence typically coincides with maturity (McShane 1995a, Prince et al. 2008).

Maturity

Maturity is specified as an ogive:

$$f_l = (1 + \exp(-\ln(19)(l - l_{50}^{mat})/\phi^{mat}))^{-1} \quad (5)$$

with centre and width parameters l_{50}^{mat} and ϕ^{mat}. Values for these parameters employed for each reef were derived from the closest analogous reef examined in the maturity survey data of Dixon (unpublished).

Recruitment processes

The recruitment by size-class, year and season is given by:

$$R_{t,l} = \omega_l \sum_{t'<t} \theta_{(t-t')} \frac{(B_{t'}^S / B_{-\infty}^S) e^{\varepsilon_t}}{\tilde{\alpha} + \tilde{\beta}(B_{t'}^S / B_{-\infty}^S)} \quad (6)$$

where

ω_l is the fraction of the recruitment that occurs to size-class *l,* with $\sum_l \omega_l = 1$. Here we use $\omega_l = 0.1$ for the first 5 classes, $\omega_l = 0.06$ for the next 5 classes, $\omega_l = 0.02$ for a further 10 classes and $\omega_l = 0$ for all larger sizes.

$\theta_{(t-t')}$ is the weighting from spawning in year *t'* to recruitment in year *t,* with $\sum_{t'<t} \theta_{(t-t')} = 1$; here we use $\theta = \{0, 0, 0.9, 0.1\}$,

$\tilde{\alpha}$, $\tilde{\beta}$ are the parameters of the Beverton-Holt stock-recruitment relationship, defined in terms of the "steepness" of the relationship, *h*, and the virgin recruitment, $R_{-\infty}$:

$$\tilde{\alpha} = \frac{(1-h)}{4hR_{-\infty}} \quad and \quad \tilde{\beta} = \frac{(5h-1)}{4hR_{-\infty}}$$

i.e. $hR_{-\infty} = \frac{0.2}{\tilde{\alpha} + 0.2\tilde{\beta}}$ and $R_{-\infty} = \frac{1}{\tilde{\alpha} + \tilde{\beta}}$.

B_t^S is the mature biomass corresponding to the recruitment during year *t*:

$$B_t^S = \sum_l w_l \, f_l \, (N_{t',l}^c + N_{t',l}^{\tilde{c}}) \tag{7}$$

ε_t is the 'recruitment residual' for year *t*. In the present work, these residuals are not estimated and we set $\varepsilon_t = 0$ for the historical period that the model is estimated against. However, fluctuations in ε_t are included in the forward simulations for the post-viral recovery period.

Initial conditions

The size-structure in years prior to the commencement of fishing is assumed to correspond to deterministic equilibrium in the absence of fishing mortality, and this size structure (which is calculated via matrix inversion) is used as an initial state for the model.

3.3 Bayesian analysis

The Metropolis algorithm is used to obtain Markov Chain Monte Carlo (MCMC) samples from the un-normalised posterior distribution

$$\pi \propto L \prod_i \Pr(y_i),$$

where $\mathbf{y} = \{h, R_{-\infty}, l_{50}, \phi, \delta_{\Delta l}\}$ is the model parameter vector, $\Pr(y_i)$ is the prior distribution for y_i and $L = L_A L_{LF} L_{Fp} L_{Bp}$ is a likelihood function comprising terms described below.

Abundance (Independent Survey)

$$\ln L_A = -\sum_t [\ln \sigma_t + \frac{1}{2\sigma_t^2} (\ln A_t - \ln(\hat{q} \sum_l S_l^r N_{t,l}))^2] \tag{8}$$

where A_t is the observed abundance of size interval in year t,

S_l^r is the selectivity of the fishery-independent survey for size-class l,

σ_t is the either a given standard error or the standard error from the data and

$$\hat{q} = \exp[\frac{1}{n}\sum_{y}(\ln A_{l,t} - \ln(\sum_{l \in l'} S_l^r N_{l,t}))] .$$

For the present work, the survey selectivity S_l^r was taken to be uniform for $l \geq 80$mm and zero for $l < 80$mm.

Length frequency

We use the robust likelihood function of Fournier *et al* (1998):

$$\begin{aligned} \log L_{LF} &= -0.5\sum_t \sum_l \log[2\pi(\xi_{l,t} + 0.1/I)] - \sum_t I \log(\tau_t) \\ &+ \sum_t \sum_l \log[\exp\{-\frac{(\rho_{l,t}^{obs} - \rho_{l,t}^{pred})^2}{2(\xi_{l,t} + 0.1/I)\tau_t^2}\} + 0.01] \end{aligned} \quad (9)$$

where $r_{l,t}^{obs}$ is the observed proportion of animals in length class *l* and year *t,*

$r_{l,t}^{pred}$ is the predicted proportion of animals in length class *l* and year *t,*

$x_{l,t} = (1 - r_{l,t}^{obs}) r_{l,t}^{obs}$,

$\tau_t^2 = 1/\min(S_t, N_{eff})$,

S_t is the sample size for the length frequency data for year *t*,

N_{eff} is the effective sample size , and

I is the number of length classes in the sample.

Penalties

A penalty term is applied to the fishing exploitation rate F_t , penalizing values close to 1:

$$L_{Fp} = \prod_t \left(1 + e^{100(F_t - 0.98)}\right)^{-1},$$

where the product is over all catch years. Similarly, the ratio of spawning biomass in the reference year to spawning biomass for the virgin population, that is the ratio $B_{2000}^s / B_{-\infty}^s$, is subject to a penalty term:

$$L_{Bp} = \left(1 + e^{100\left(B_{2000}^s / B_{-\infty}^s - 0.4\right)}\right)^{-n} \left(1 + e^{-100\left(B_{2000}^s / B_{-\infty}^s - 0.2\right)}\right)^{-n},$$

where n is an adjustable parameter and we have used $n = 10$. This term penalizes values lying outside a biologically reasonable range (0.2,0.4) for an exploited population that has not crashed.

Priors and parameters

Uniform priors were used for the five model parameters:

Table 1. Priors used in model estimation.

Parameter	Prior Distribution
h	U(0.45, 0.75)
$R_{-\infty}$	U(5×10^4, 1.3×10^6)
l_{50}(mm)	U(l_{50}^{mat}-15, l_{50}^{mat}+30)
ϕ(mm)	U(10, 50)
$\delta_{\Delta t}$	U(0.6, 1.4)

Natural mortality was taken to be uniform across size classes, with a value $M_l = 0.2$. This is a generally agreed value for the exploitable component of abalone populations in the absence of more specific information. There a few quantitative studies that have estimated M for blacklip abalone, but a study undertaken by Beinssen & Powell (1979) in Eastern Victoria and another by Nash (1992) corroborate our assumption. Shepherd & Breen 1992 reviewed abalone mortality estimates from many studies, including that of Beinssen and Powell. Their tabulated values of instantaneous rates of natural mortality for various species around the world ranged from 0.07 for adult *H. fulgens* to 10.2 for post-larval *H. rubra* spat (< 5 months old). However, values between 0.15 and 0.4 were more typical among estimates for abalone of several years or older. Since we are modelling populations from 52 mm onwards it is reasonable to assume that M is at the lower end of the range.

3.4 Viral impact simulations

Once the model parameters were estimated against historical data, forward simulations of population dynamics were conducted at the estimated values, with viral impacts of varying severity imposed at $t = 2006$ and zero fishing ($F_t = 0$) for $t \geq 2006$. Additionally, Monte Carlo simulations were conducted in which recruitment residuals ε_t for $t \geq 2006$ were (independently) sampled from a normal distribution, with mean zero and $\sigma = 0.7$, resulting in distributions of time-to-recovery for each reef across a range of viral impacts. This variance for ε_t implies that halving or doubling of recruitment from the mean rate is approximately a one-sigma event, which certainly does not overstate natural variability and may, in fact, understate the temporal variation observed in abalone recruitment.

Since the model does not explicitly track the size structure below 52mm, correctly implementing viral impact (i.e. uniformly across sizes) requires applying the viral mortality factor to biomass terms in the recruitment function (Eq. 6) that relate post-impact recruitment to pre-impact biomass. Terms relating post-impact recruitment to biomass from the impact year (or later) need no modification, as the biomass calculation already reflects the viral impact.

Post-viral fishing impact

We examine the effect of a resumption of fishing on recovery times for a range of viral impacts and fishing levels, using model parameters estimated for the baseline scenarios. Population dynamics simulations are conducted in which an initial zero-fishing period (immediately after the viral impact) is followed by fishing at levels much reduced from pre-virus fishing. A variation is considered in which IUU fishing continues at pre-virus level throughout the recovery period.

4. Results

Model estimation

Observation of MCMC traces for the model parameters, during estimation for each of the IUU scenarios, indicated that in the worst cases amongst all parameters and reefcodes, obvious transients had decayed after 4×10^4 iterations. Longer runs (10^6 iterations with burn-in of 10^5 iterations) were then conducted and convergence of posterior means was assessed by comparison of means from the full run with those evaluated after 4×10^5 iterations (i.e comprising averages of one third the number of iterations). Worst-case differences between these posterior mean estimates were at the 2% level. Parameter estimates and coefficients of variation, obtained from the full MCMC run, are given in Tables 2 and 3.

Table 2. Parameter estimates and coefficients of variation for the baseline IUU scenario.

Reefcode	$\overline{h}$	CV[h]	$\overline{R_{-\infty}}$	CV[$R_{-\infty}$]	$\overline{l_{50}}$(mm)	CV[l_{50}]	$\overline{\phi}$(mm)	CV[ϕ]	$\overline{\delta_{\Delta t}}$	CV[$\delta_{\Delta t}$]
Julia Percy I	0.48	0.057	5.8×10^4	0.047	120	0.005	21.2	0.058	1.02	0.03
Crags	0.46	0.019	8.4×10^5	0.04	118	0.01	24.1	0.046	1.12	0.031
Mills	0.53	0.067	1.4×10^5	0.042	119	0.005	23.7	0.032	1.37	0.018
Killarney	0.63	0.118	4.3×10^5	0.119	108	0.008	18.8	0.049	1.19	0.044
Cutting	0.51	0.062	1.9×10^5	0.028	125	0.0014	23.0	0.028	1.40	0.005

Table 3. Parameter estimates and coefficients of variation for the high IUU scenario.

Reefcode	$\overline{h}$	CV[h]	$\overline{R_{-\infty}}$	CV[$R_{-\infty}$]	$\overline{l_{50}}$(mm)	CV[l_{50}]	$\overline{\phi}$(mm)	CV[ϕ]	$\overline{\delta_{\Delta t}}$	CV[$\delta_{\Delta t}$]
Julia Percy I	0.47	0.037	7.3×10^4	0.036	120	0.005	21.1	0.057	1.01	0.029
Crags	0.45	0.005	1.05×10^6	0.027	117	0.011	23.5	0.049	1.18	0.028
Mills	0.49	0.052	1.7×10^5	0.039	119	0.005	23.8	0.031	1.38	0.017
Killarney	0.54	0.059	5.6×10^5	0.068	109	0.009	19.4	0.048	1.15	0.036
Cutting	0.46	0.024	2.6×10^5	0.039	121	0.012	21.1	0.052	1.37	0.017

It is evident that the time-series of abundance data driving the model, in conjunction with the data it is estimated against, the prior distributions and the constraints imposed by biomass and fishing penalty terms, have combined to yield highly informative posterior distributions. In Fig. 5 we show fitted length frequency and relative abundance curves for Crags, along with the corresponding observed data. The high information content in the length-frequency data results in a good fit and these data strongly influence the model. In contrast, the fitted relative abundance curve only weakly follows the observed trend data, which is sparse and has large coefficient of variance (SE/mean = 0.2). These observations hold also for the other reefs and for the high IUU scenarios. Note that the abrupt drop in abundance due to the virus in 2006 appears to offer an example where the fitted abundance closely follows the observed trend, however this is an artifact because the final point in the fitted curve depends on the imposed viral mortality scenario (80% in this case), rather than on the automatic evolution of the population dynamics model.

Recovery simulations

The estimates in Tables 2 and 3 were derived from past behaviour of the fishery; we now apply the population dynamics model, operating at these estimated values, to explore the future, specifically to examine recovery from the high-mortality viral event of 2006. Note that amongst the reefs examined here, Lady Julia Percy Island is currently believed to have remained disease free. Nevertheless, simulations for this reef, using hypothetical viral impacts in 2006, are included here for reference, since the virus may ultimately reach this island, despite its geographical isolation.

The Crags is the most productive and hence the most important of the five reefs from a fisheries management viewpoint; accordingly we begin with the baseline IUU scenario for this reef, assuming a high (but plausible) viral mortality of 80%. Fig. 6 shows the resulting size-structured abundance trajectory, beginning with the historical period and then projecting into the post-viral recovery period (assuming zero fishing); the important corresponding biomass trajectories appear in Fig. 7.

The between-reef variation in depletion trajectories and associated post-viral response is illustrated in Fig. 8, showing size-structured emerged abundance for Julia Percy Island, Mills, Killarney and Cutting, which may be compared with the emerged abundance plot for Crags, appearing in Fig 6.

The effect of varying viral impact is investigated in Fig. 9, where recovery from a range of viral impacts is shown in the baseline IUU scenario for Crags.

The management criterion for recovery is that biomass attains 90% of its value in some reference year, which is taken to be the year 2000. This allows us to define recovery time as the number of years after the viral event that the population first exceeds 90% of B_{2000} (the biomass in 2000). Table 4 below gives results for simulated recovery times for all five reefs across a range of ten viral impacts. These simulations

used model parameters estimated in the baseline IUU scenario (Table 2). Zero viral impacts are included because a population that was in steep decline prior to the virus could require a non-zero recovery time to reach 90% of B_{2000}. All the simulations were then repeated for the high IUU scenario, with the results appearing in Table 5.

Table 4. Recovery times for the baseline IUU scenario.

	Mortality impact of viral event									
Reef	**90%**	**80%**	**70%**	**60%**	**50%**	**40%**	**30%**	**20%**	**10%**	**0**
Julia Percy I	19	14	11	8	6	4	3	1	1	0
Crags	20	14	10	8	5	3	2	1	0	0
Mills	18	13	10	8	6	4	2	1	0	0
Killarney	15	11	8	6	5	3	2	1	0	0
Cutting	20	15	11	9	6	4	3	1	0	0

Table 5. Recovery times for the high IUU scenario.

	Mortality impact of viral event									
Reef	**90%**	**80%**	**70%**	**60%**	**50%**	**40%**	**30%**	**20%**	**10%**	**0**
Julia Percy I	19	14	10	8	6	4	2	1	0	0
Crags	19	13	9	6	4	2	1	0	0	0
Mills	20	14	11	8	6	4	2	1	0	0
Killarney	19	13	10	7	5	3	2	1	0	0
Cutting	24	17	13	10	8	5	3	1	0	0

Comparing Tables 4 and 5, we see that for heavy viral impacts, the typical effect of higher IUU is to substantially delay recovery (Killarney and Cutting) or to slightly advance recovery (Julia Percy Island and Crags). For mild viral impacts (30% or less), the high IUU scenario recovers more quickly, where a difference exists.

This pattern can be directly related to trade-offs between the estimated Beverton-Holt parameters (see Tables 2 and 3). In all cases, the high IUU scenario resulted in substantially larger $R_{-\infty}$ estimates, i.e. the model required a larger population to supply the heavier early catch. However, in all cases a somewhat lower estimate for h was obtained, indicating the necessity of a trade-off within the likelihood function (eg to satisfy the biomass penalty). In the case of reefs 3.10 and 3.11, this reduction in h was substantial (of order 10%) and this results in the delayed recoveries observed for those reefs.

A major cause of variation in abalone population dynamics is the highly erratic settlement and recruitment influx at any given site. In the population dynamics model, this variation is represented by the recruitment residuals ε_t. The results of Monte

Carlo simulations in which the ε_t fluctuate during the recovery period are given as recovery-time probability distributions (Fig. 10) for a range of viral impacts in the baseline IUU scenario.

Impact of post-viral fishing

Thus far our analysis has assumed the complete absence of legal fishing in the post-virus recovery period. We now consider recovery delays, relative to the baseline recovery times in Table 4, resulting from a partial resumption of fishing in 2010, i.e. four years after the viral event. The resumed catch is a fraction (ranging from 5% to 20%) of average pre-viral catch over the 5 years prior to the viral event). It is assumed that the post-virus IUU catch is a proportion (5%) of the commercial catch; in particular, this assumption means that during the first three post-virus years, both the commercial and IUU catches are zero. Simulations using the baseline estimated model (Table 2) for a range of post-virus catch levels and viral impacts resulted in the recovery delays shown in Table 6.

Reef	Fishing level	Mortality impact of viral event 90%	80%	70%	60%	50%	40%	30%
Julia Percy I.	**5%**	6	3	1	1	1	0	0
	10%	14	7	4	3	2	1	0
	15%	19	14	9	5	3	2	0
	20%	25	20	16	11	6	3	0
Crags	**5%**	3	1	1	0	0	0	0
	10%	5	2	2	0	1	0	0
	15%	9	4	2	1	1	0	0
	20%	13	6	3	1	1	0	0
Mills	**5%**	3	1	1	0	0	0	0
	10%	6	3	2	1	0	0	0
	15%	8	6	4	2	1	0	0
	20%	10	8	6	3	2	1	0
Killarney	**5%**	1	1	1	1	0	0	0
	10%	3	1	1	1	0	0	0
	15%	4	2	2	2	0	0	0
	20%	5	3	3	2	1	0	0
Cutting	**5%**	7	5	4	3	2	2	1
	10%	10	6	5	4	2	2	1
	15%	13	8	6	4	3	2	1
	20%	15	10	7	5	3	2	1

Table 6. Recovery delays (yrs) due to resumption of fishing 4 years after viral impact, assuming proportional IUU catch (5% of commercial).

Recovery delays are substantially longer for Julia Percy Island than for the other reefs, whilst those Killarney are the shortest. These observations can be related to the parameter estimates in Table 2: the main distinguishing feature for reef Julia Percy Island is that it has the slowest growth parameter $\delta_{\Delta t}$, which will reduce productivity, whilst Killarney has the largest Beverton-Holt "h" parameter, which will tend to enhance recovery under fishing pressure.

Delayed recovery due to fishing is illustrated in Fig. 11 for the case of a 90% viral impact occurring in reef Crags, with fishing resumed at 20% of pre-virus levels in 2010. Comparison of the size-structured abundance plot with the 90% case in Fig. 9 shows that the steady exponential-type growth in the no-fishing case is interrupted for approximately 10 years in the 20% fishing case, during which time the exploited biomass fraction (F) remains essentially at 1. Thus almost all biomass above the legal minimum length (LML) is removed by fishing during that period, until eventually the accumulating biomass below the LML becomes sufficient to overcome the fishing pressure. This is signified by a rapid decrease in F and the resumption of an exponential-type recovery.

Finally, we consider the possibility that instead of being proportional to the post-virus catch, the IUU catch continues throughout the recovery period at pre-virus levels (i.e. at 5% of the pre-virus commercial catch). This amounts to assuming that the IUU catch is independent of the commercial effort. The results of corresponding simulations are presented in Table 7, which includes cases of zero commercial catch because the IUU catch alone causes significant delays relative to the baseline scenario in Table 4. Comparison of Tables 6 and 7 makes it clear that for high viral impacts, the effect of a constant IUU catch, albeit small by pre-virus standards, can drastically impede recovery.

Reef	Fishing level	Mortality impact of viral event 90%	80%	70%	60%	50%	40%	30%
Julia Percy I.	**0**	8	4	2	2	1	1	0
	5%	15	9	5	3	2	2	0
	10%	20	15	10	6	4	3	0
	15%	26	20	16	11	7	4	0
	20%	32	27	23	19	13	7	0
Crags	**0**	3	2	1	0	0	0	0
	5%	6	3	2	1	1	0	0
	10%	10	4	3	1	1	0	0
	15%	13	6	4	2	1	0	0
	20%	16	8	5	2	2	0	0
Mills	**0**	4	2	1	1	0	0	1
	5%	6	4	3	1	1	1	1
	10%	8	6	4	2	2	1	1
	15%	10	8	6	4	2	1	1
	20%	12	10	8	6	4	2	1
Killarney	**0**	2	1	1	1	0	0	0
	5%	3	2	2	1	0	0	0
	10%	4	3	2	2	1	0	0
	15%	5	4	3	2	1	0	0
	20%	6	5	4	3	1	0	0
Cutting	**0**	8	5	4	3	2	2	1
	5%	11	7	5	4	2	2	1
	10%	13	8	6	5	3	2	1
	15%	15	10	7	5	3	3	1
	20%	17	12	9	6	4	3	1

Table 7. Recovery delays (yrs) due to resumption of fishing 4 years after viral impact, combined with an IUU catch remaining at pre-virus levels for the entire recovery period.

5. Discussion

5.1 Biological processes that appear to determine outcomes

The processes that lead to the numbers and size composition of abalone that become visible to divers as the stocks recover are likely to be heavily masked by the pattern of emergence of abalone from cryptic habitat. Thus we focus first on the numbers of all the mature size-classes, before and after the disease impact. The simulation for The Crags, one of the first productive areas hit by AVG, if the mortality were 80% is

shown in Figures 6 and 7. In general, increasing size limits on a reef by reef basis, by as much as 10mm above the LML in some instances, and progressively decreasing the Zone's TACC from the original 280 tonnes to 221 tonnes, meant that reefs within the study area had reached a fairly stable equilibrium between harvesting of larger adults and recruitment to larger sizes, prior to the disease impact. This balance is characterised by relatively low proportions of the largest size classes (>130 mm). On many reefs the voluntary increases in harvest size limits between 2002 and 2007 had increased numbers of 130-140 mm and larger abalone. As fecundity increases roughly with the cube of length, and thus in proportion to biomass, the numbers of these larger abalone are most important in determining the how many recruits grow into the modelled stock each year. If smaller adult blacklip abalone increase growth rather than fecundity when density is reduced, as Dixon and Day (2004) suggest for greenlip abalone, then larger abalone would influence recruitment even more strongly at low population densities.

Accurate surveys of juvenile abalone are problematic, with much potential for underestimation due preferences for habitat within deep crevices and under boulders.
As the model considers abalone >52 mm and juvenile growth is variable, the recruitment each year into the modelled stock depends on juveniles produced in 3 previous years, so that recruitment is related to a weighted sum of total adult biomass in each of the 3 prior years. This, together with variable growth of abalone in the modelled size classes smoothes the changes in recruitment to mature sizes over time.

As we assume the virus impacts all sizes equally, both the modelled stocks and the recruitment of juveniles from previous years is reduced after the disease impact. A 30% stock reduction (Figure 9) leads to fairly rapid subsequent exponential increases in adult stocks, partly because growth of the remaining larger adults rapidly increases total fecundity, and partly because the stock-recruitment function dictates there will be more recruits per unit mature biomass at low density. The growth rate of larger abalone slows, so that abalone accumulate faster in the 130–140 and >140 mm size classes than for smaller sizes, and they are not removed as the reefs remain closed to fishing (in these simulations). Thus the numbers of these two largest size classes exceed the pre-virus numbers within 2 years, even though the total numbers of mature abalone do not recover until 7 years after the disease impact. This effect, plus the fact that the divers see mostly only the size classes over 110 mm, in which most are not cryptic, means that the recovery appears to be much faster (4 years) in the diver's eye view of the reef (Figure 9),

Note that the model does not take into account any density-dependent growth, nor any decrease in the size at emergence from crevices once substantial numbers of emergent adults die, nor any effects of aggregation of remaining abalone into the best habitat patches, where commercial divers will focus their search. These three mechanisms would all increase the apparent abundance of abalone on reefs to commercial divers, and all probably occur to some extent (Dixon and Day 2004, McAvaney et al. 2004, Officer et al. 2001), but we have insufficient data to estimate such effects and thus incorporate them into our model.

If the disease removes 80% of each size-class (Figure 6), then the growth of the reduced numbers of juveniles and smaller adults adds to the numbers >130 mm more slowly, but with the same pattern, so that numbers of these large adults reach pre-

virus levels after 8 years, while the total numbers of adults recover to pre-virus levels only after about 20 years. The diver's eye view however, would suggest that the stocks had recovered to 2000 levels after 17 years (Figure 9).

The reefs modelled differ in the abundance and size-distribution of abalone present before the disease impact, as well as in growth rates. Thus the number of years required to ensure a high probability of recovery varies between reefs (Figure 10). Reef area 3.10, for example, recovers more rapidly than other areas. But these differences are small in comparison to the effect of the mortality rate that the disease inflicts on a reef. This emphasizes the importance of accurate measurement of these mortality rates as the disease spreads further into the Central Zone, or perhaps in other areas. The only means to do this appears to be surveys prior to, and soon after the disease event on each reef area.

The simulations of each reef are informed by estimates of catch histories, and one of the largest uncertainties is the degree of illegal catch in each area in the past. If the reef stocks sustained larger catches in the past than we have estimated, then the stock reduction by the virus is a smaller percentage of the total reduction of the virgin biomass since the fishery began. Thus one might expect less compensatory response in recruitment to the disease reduction, as is shown for reefcodes 3.10 and 3.11 in Tables 4 and 5, where the illegal or unreported catch is assumed substantially higher than the reported catch.

5.2 Implications for future management of the resource

Future management of disease-affected abalone must adapt to the changing circumstances, and adopting a precautionary approach will allow maximum potential for stock recovery. This approach is mandated by the observation that no examples are known of abalone populations recovering from catastrophic impacts such as have occurred in the abalone fisheries of Victoria's Western and Central zones. Indeed the balance of international evidence points towards the contrary, so these fisheries are in dangerous territory. This need not mean that recovery cannot occur.

However, the modelling results presented here confirm the above precautionary view and suggest that unless it is known with certainty that disease-induced mortalities have been moderate (less than 40%), then any resumption of fishing in the near term risks the future of the fishery. Acquisition of accurate mortality data is the only basis upon which fishing can recommence in the short term (within 5 years) and in many instances, such as for some among those reefs considered in our study, the opportunity has passed. The simulation results provide guidance, but their validity is conditional on myriad assumptions as well as on the accuracy of data employed. We already know that catches early in the fisheries' history were higher than those reported officially, but how much higher remains conjecture. Growth is highly variable over small spatial scales and density dependence effects together with size structure and persistence of habitat will play roles in determining the rate, if any, of recovery. The extent of the contemporary illegal catch is uncertain, particularly given the unprecedented closure of the fisheries. The results given here show that even

small illegal catches can significantly degrade recovery where the viral impact is high, with clear implications for the enforcement aspects of managing these fisheries.

Design of future data collection strategies within Victoria and its neighbouring states of South Australia, New South Wales and Tasmania (despite its separation from the mainland by Bass Strait) should be focused on acquisition of base line data and a preparedness to sample disease affected populations as the disease is occurring and subsequently at a frequency that identifies its persistence. For instance, enumeration and measurement of morbid and dead abalone and evacuated shells may prove invaluable. Surveys such as these are expensive and industry should consider how it might contribute to the provision of comprehensive spatially resolved data such as size structure and abundance that will be responsive to mortality. As mentioned in the introduction, commercial abalone divers, driven by an imperative to earn a living, are already making assertions that the resource has recovered sufficiently to resume harvesting. Our study shows that although they are accurately reporting what they, but that appearances in this instance are deceptive.

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References

Andrew, N.L., Y. Agatsuma, E. Ballesteros, A.G. Bazhin, E.P. Creaser, D.K.A. Barnes, L.W. Botsford, A. Bradbury, A. Campbell, J.D. Dixon, S. Einarsson, P. Gerring, K. Hebert, M. Hunter, S.B. Hur, C.R. Johnson, M.A. Juinio-Menez, P. Kalvass, R.J. Miller, C.A. Moreno, J.S. Palleiro, D. Rivas, S.M.L. Robinson, S.C. Schroeter, R.S. Stenecj, R.I. Vadas, D.A. Woodby, & Z. Xiaoqi. 2002. Status and management of world sea urchin fisheries. *Oceanography and Marine Biology Annual Revue* 40, 343–425.

Appleford, P. 2007. 2nd Abalone Virus Scientific and Management Forum 2 October 2007. Fisheries Victoria, Department of Primary Industries. http://www.dpi.vic.gov.au/DPI/nrenfaq.nsf/childdocs/-D45F5C300E5D2ED54A2567D700236463-6E6F5C6DF9868F86CA25741F001C5236-3458DE4A698E42F5CA25741E00834266?open Accessed on 6 June 2008.

Babcock, R. & J. Keesing. 1999. Fertilization biology of the abalone *Haliotis laevigata*: laboratory and field studies. *Canadian Journal of Fisheries and Aquatic Sciences 56*: 1668–1678.

Bardos, D.C. 2005. Probabilistic Gompertz model of irreversible growth. *Bulletin of Mathematical Biology* 67: 529–545.

Beinssen, K. & D. Powell. 1979. Measurement of natural mortality in a population of blacklip abalone *Notohaliotis ruber*. *Rapports et Proces-Verbaux des Reunions. Conseil International pour l'Exploration de la Mer* 175: 23–26.

Bergquist, D. 2007. Sustainability and local people's participation in coastal aquaculture: regional differences and historical experiences in Sri Lanka and the Philippines. *Environmental Management*. 40: 787–802.

Cook, P. 1998. The current status of abalone farming in South Africa. *Journal of Shellfish Research* 17: 601–602.

Day, R.W. & A.E. Fleming. 1992. The determinants and measurement of abalone growth. pp.141–168. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Próo (eds.). Abalone of the World: Biology, Fisheries and Culture. Blackwell, Oxford, U.K.

Day, R., P Gilmour & S. Huchette. 2004. Effects of density and food supply on postlarval abalone: behaviour, growth and mortality. *Journal of Shellfish Research. 23*: 1009–1018.

Day R, Dowell A, Sant G, Klemke J & Shaw C (1995) Patchy predation: foraging behaviour of *Coscinasterias calamaria* and escape responses of *Haliotis rubra*. *Mar Freshw. Behav. Physiol*. **26**:11-33.

Day, R.W. & S.A. Shepherd. 1995. Fisheries biology and ecology of abalone: Introduction. *Marine Freshwater Research 46*: iii–v.

de Waal, S. & P.A. Cook. 2001. Use of a spreadsheet model to investigate the dynamics and the economics of a seeded abalone population. *Journal of Shellfish Research*. 20: 863–866.

Dixon, C.D. Size at maturity surveys in Victoria, November 2000 – June 2003.
Department of Primary Industries, Victoria, unpublished.

Dixon, C.D. & R.W. Day. 2004. Growth responses in emergent greenlip abalone to density reductions and translocations. *Journal of Shellfish Research. 23*: 1223–1228.

Dixon, C. D., H. K. Gorfine, R. A. Officer & M. Sporcic. 1998. Dispersal of tagged blacklip abalone, *Haliotis rubra*: Implications for stock assessment. *J. Shellfish Res.* 17: 881–887.

Fisheries Victoria. 2002. Abalone Management Plan. Fisheries Victoria, East Melbourne. 66 pp.
http://www.dpi.vic.gov.au/DPI/nrenfaq.nsf/LinkView/9F09A1B4418E935BCA256C55001EB9A9F5F3C3DA915AFBE4CA256C6F0016CA60 Accessed on 6 June 2008

Fisheries Victoria. 2008.
http://www.dpi.vic.gov.au/DPI/nrenfaq.nsf/LinkView/F6E3928C98353339CA25741E007DA04A6E6F5C6DF9868F86CA25741F001C5236 Accessed on 6 June 2008.

Fournier, D.A., J. Hampton, & J.R. Sibert. 1998. MULTIFAN-CL: a length-based age-structured model for fisheries stock assessment, with applications to South Pacific albacore, *Thunnus alalunga*. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 2105–16.

Geiger, D. L. 2000. Distribution and biogeography of the Haliotidae (Gastropoda: Vetigastropoda) world-wide. *Bollettino Malacologico* 35: 57-120.

Gordon, R. & P.A. Cook. 2001 World abalone supply, markets and pricing: Historical, current and future, *Journal of Shellfish Research*. 20: 567–570.

Gorfine, H.K., D.A. Forbes & A.S. Gason. 1998. A comparison of two underwater census methods for estimating the abundance of the commercially important blacklip abalone, *Haliotis rubra*. *Fishery Bulletin* 96: 438–450.

Gorfine, H.K., R. Tailby, F. Gant, M. Donaldson & I. Bruce. 2002. Estimation of illegal catches of Australian abalone: Development of desk-based methods. FRDC Project 2000–112 final report. Marine and Freshwater Resources Institute, Queenscliff, Victoria, Australia.

Gorfine, H., B. Taylor, M. Cleland, M. Haddon, A. Punt, A., D. Worthington & I. Montgomery. 2005. Development of a spatially-structured model for stock assessment and TAC decision analysis for Australian Abalone fisheries. Final report to the Fisheries Research and Development Corporation. Project No. 1999–116. Primary Industries Research Victoria, Queenscliff, Australia. 108 pp.

Gorfine, H.K., Taylor, B.L. & Walker, T.I. 2001. Triggers and targets: What are we aiming for with abalone fisheries models in Australia? *Journal of Shellfish Research*. 20:803–811.

Hahn, K.O. (ed.). 1989. Handbook of Culture of Abalone and Other Marine Gastropods. CRC Press, Florida. 348 pp.

Hancock, B. 2000. Genetic subdivision of Roe's abalone, *Haliotis roei* Grey (Mollusca: Gastropoda), in south-western Australia. *Marine and Freshwater Research* 51:679–687.

Hart, A. M. & H. K. Gorfine. 1997. Abundance estimation of blacklip abalone (*Haliotis rubra*) II. A comparative evaluation of catch-effort, change-in-ratio, mark-recapture and diver-survey methods. *Fisheries Research* 29:171–183.

Hart, A. M., H. K. Gorfine & M. C. Callan. 1997. Abundance estimation of blacklip abalone (*Haliotis rubra*) I. An analysis of diver-survey methods for large-scale monitoring. *Fisheries Research* 29:159–169.

Hooper, C., P. Hardy-Smith & J Handlinger. 2007 Ganglioneuritis causing high mortalities in farmed Australian abalone (*Haliotis laevigata* and *Haliotis rubra*). *Australian Veterinary Journal* 85: 188–193.

Huchette, S.M.H. 2003. Density-dependence in the early life stages of abalone. PhD thesis, Univ. Melbourne.

Johnson, C.R., S.D. Ling, D.J. Ross, S.A. Shepherd, & K. Miller. 2005. Establishment of the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania: First assessment of potential threats to fisheries. Final report to the Fisheries Research and Development Corporation. Project No. 2001–044. School of Zoology and Tasmanian Aquaculture & Fisheries Institute, Hobart, Tasmania. 79 pp.

Lindberg, D.R. 1992. Evolution, distribution and systematics of Haliotidae. pp. 3–18. In: S. A. Shepherd, M. J. Tegner & S. A. Guzmán del Próo (eds.). Abalone of the World: Biology, Fisheries and Culture. Blackwell, Oxford, U.K.

McAvaney, L.A., R.W. Day, C.D. Dixon & S.M. Huchette. 2004. Gonad development in seeded Haliotis laevigata: growth environment determines initial reproductive investment. *Journal of Shellfish Research* 23: 1213–1218.

McBride, S.C. 1998. Current status of abalone aquaculture in the Californias. *Journal of Shellfish Research* 17: 593–600.

McShane, P.E. 1990. The Fisheries Ecology of Victorian Abalone. Ph.D. thesis, LaTrobe University, Melbourne, Australia.

McShane, P.E. 1991. Density dependent mortality of recruits of the abalone *Haliotis rubra* (Mollusca: Gastropoda). *Marine Biology* 110,110: 385–389.

McShane, P.E. 1992. Early life history of abalone: a review.In *Abalone of the world: biology, fisheries and culture* (ed. S. A. Shepherd, M. J. Tegner and S. A. Guzmán del Próo), pp. 120–140. Blackwell: Oxford.*In*: S.A. Shepherd, M.J. Tegner & S.A. Guzmán del Próo (eds.). Abalone of the World: Biology, Fisheries and Culture. Blackwell, Oxford, U.K.

McShane, P. E. 1995a. Recruitment variation in abalone: its importance to fisheries management. *Marine Freshwater Research* 46:555–570.

McShane, P. E. 1995b. Estimating the abundance of abalone: the importance of patch size. Marine and Freshwater Research 46:657–662.

McShane, P. E. 1996. Patch dynamics and effects of exploitation on abalone (*Haliotis iris*) populations. *Fisheries Research* 25:191–199.

McShane, P.E., K.P. Black & M.G. Smith. 1988a. Recruitment processes in Haliotis rubra (Mollusca: Gastropoda) and regional hydrodynamics in southeastern Australia imply localised dispersal of larvae. *Journal of Experimental Marine Biology and Ecology* 124: 175–203.

McShane, P. E., M. G. Smith & K. H. H. Beinssen. 1988b. Growth and morphometry in abalone (*Haliotis rubra* Leach) from Victoria. *Australian Journal of Marine and Freshwater Research* 39:161–166.

Morse, D. 2007. Nanotechnology: Daniel Morse Interview http://www.biotechmedia.com/DanMorseInterview07-23-07.html (Accessed on 14 June 2008).

Morse, D.E., N. Hooker, H. Duncan, and L. Jensen, L., 1979. g-Aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. *Science* 204: 407–410.

Nash, W.J. (1992) An evaluation of egg-per-recruit analysis as a means of assessing size limits for blacklip abalone (*Haliotis rubra*) in Tasmania. pp. 318-338. *In*: S.A. Shepherd, M.J. Tegner and S.A. Guzmán del Próo (eds). Abalone of the World: Biology, Fisheries and Culture. Blackwell, Oxford, U.K.

Officer, R. A., H. K. Gorfine & C. D. Dixon. 2001. Movement and re-aggregation of the blacklip abalone, *Haliotis rubra*, after fishing. *Journal of Shellfish Research.* 20: 771–779.

Prince, J.D. (2003). The barefoot ecologist goes fishing. *Fish and Fisheries* 4: 359–371.

Prince, J.D. 2005. Combating the tyranny of scale for haliotids: micro-management for microstocks. *Bulletin of Marine Science,* 76: 557–577.

Prince, J.D., H. Peeters, H. Gorfine, & R.W. Day. 2008. The novel use of harvest policies and rapid visual assessment to manage spatially complex abalone resources (Genus *Haliotis*). *Fisheries Research*, 94: 330–338.

Prince, J.D., T.L. Sellers, W.B. Ford & S.R. Talbot. 1987. Experimental evidence for limited dispersal of haliotid larvae (genus *Haliotis*: Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 106: 243–263.

Prince J.D., T.L. Sellers, W.B. Ford & S.R. Talbot. 1988. Confirmation of a relationship between the localized abundance of breeding stock and recruitment for *Haliotis rubra* Leach (Mollusca: Gastropoda). *Journal of Experimental Marine Biology and Ecology* 122: 91–104.

Prince, J. D., C. Walters, R. Ruiz-Avila & P. Sluczanowski. 1998b. Territorial user's rights and the Australian abalone *(Haliotis* sp.) fishery. *In*: G. S. Jamieson & A. Campbell (eds.). Proceedings of the North Pacific symposium on invertebrate stock assessment and management. *Canadian Special Publication in Fisheries and Aquatic. Sciences.* 125: 367–375.

Quinn, T. J. & R. B., Deriso. 1999. Quantitative Fish Dynamics. Oxford University Press, New York.

Shepherd, S.A. 1990. Studies on southern Australian abalone (genus *Haliotis*) XII. Long-term recruitment and mortality dynamics of an unfished population. *Australian Journal of Marine and Freshwater Research* 41: 475–492.

Shepherd, S.A. & P.A. Breen. 1992. Mortality in abalone: its estimation, variability and causes. pp.276–304. *In*: S.A. Shepherd, M J. Tegner & S.A. Guzmán del Próo, (eds.). Abalone of the World: Biology, Fisheries and Culture. Blackwell, Oxford, U.K.

Shepherd, S.A. & S. Daume. 1996. Ecology and survival of juvenile abalone in a crustose coralline habitat in South Australia. pp. 297–313. In: Watanabe, Y., Yamashita, Y. and Oozeki, Y. Survival Strategies in Early Life Stages of Marine Resources. Balkema, Rotterdam.

Shepherd, S. A. & C. Godoy. 1989. Studies on southern Australian abalone (genus *Haliotis*) XI. Movement and natural mortality of juveniles. *Journal of the Malacological Society of Australia* 10:87–95.

Shepherd, S.A, C. Godoy, & S.M. Clarke. 1992a. Studies on southern Australian abalone (genus *Haliotis*) XV. Fecundity of *H. laevigata*. *Journal of the Malacological Society of Australia* 13: 115–121

Shepherd, S.A., M.J. Tegner & S.A. Guzmán del Próo (eds.). 1992b. Abalone of the World: Biology, Fisheries and Culture. Blackwell, Oxford, U.K.

Simizu, T. and Uchino, K. 2004. Effects of extensive seeding on abalone. *Haliotis discus discus*, abundance on the Pacific coast of Boso Peninsula, Japan. *Journal of Shellfish Research,* 23: 1209–1211.

Troynikov, V.S. 1998. Probability density functions useful for parameterisation of heterogeneity in growth and allometry data. *Bulletin of Mathematical Biology* **60**, 1099–1122.60: 1099–1122.

Troynikov, V.S. and Gorfine, H.K. (1998). V. S. & H. K. Gorfine. 1998. Alternative approach for establishing legal minimum lengths for abalone based on stochastic growth models for length increment data. *Journal of Shellfish Research,* 17, 827–831.

Wang, J., Z. Guo, J. Feng, G. Liu, L. Xu, B. Chen & J. Pan. 2004. Virus infection in cultured abalone, *Haliotis diversicolour* Reeve in Guangdong Province, China. *Journal of Shellfish Research,* 23: 1163–1168.

Zhang, G., H. Que, X. Liu, & H. Xu. 2004 Abalone mariculture in China. *Journal of Shellfish Research,* 23: 947–950.

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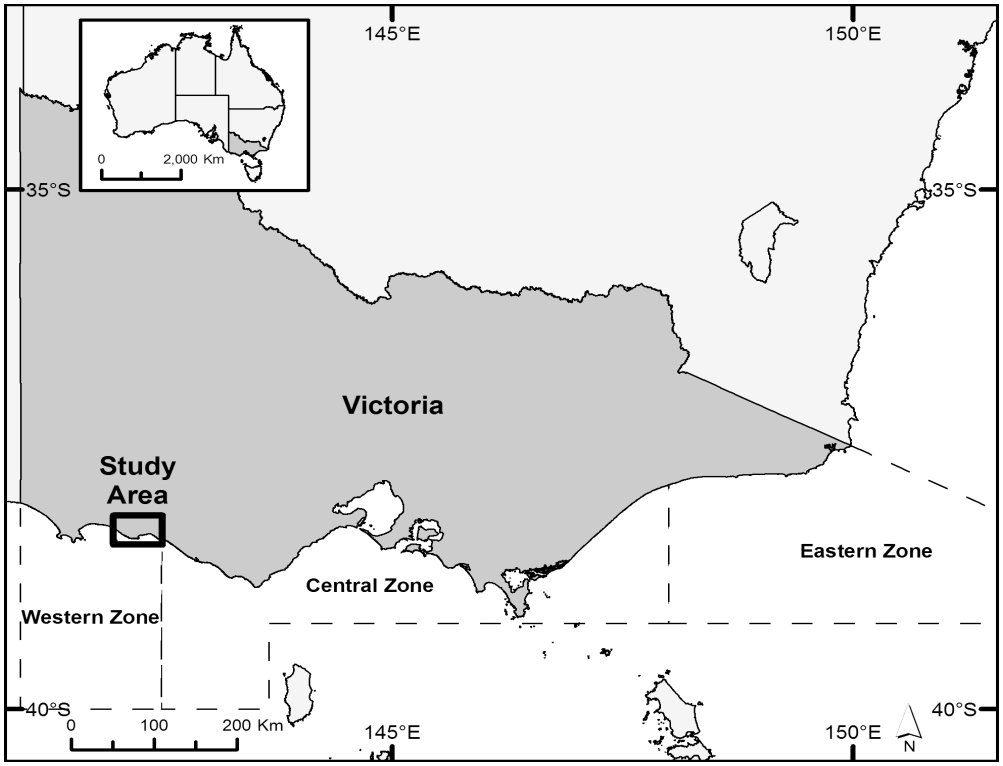


Figure 1

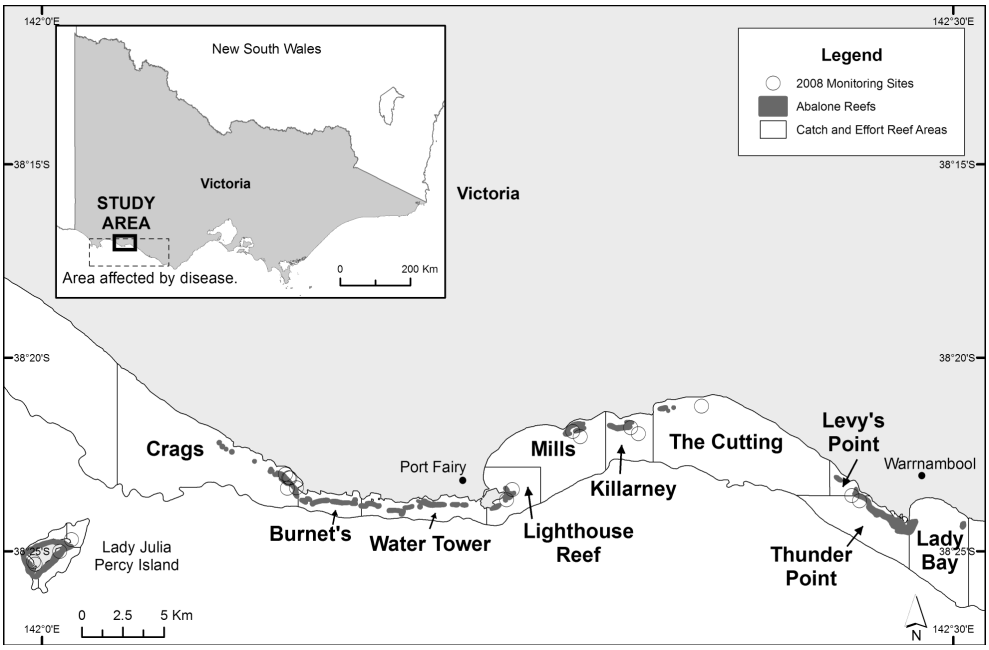
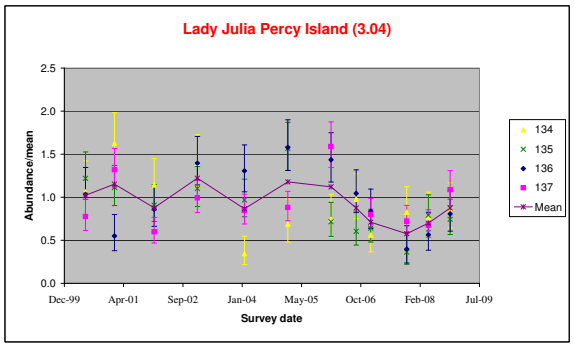
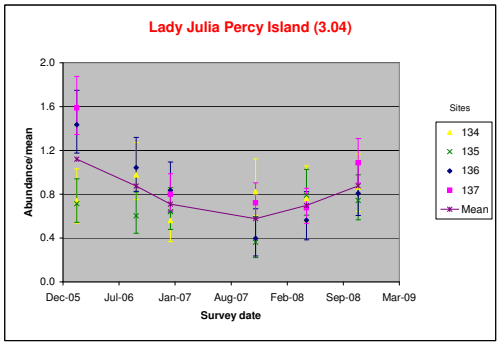
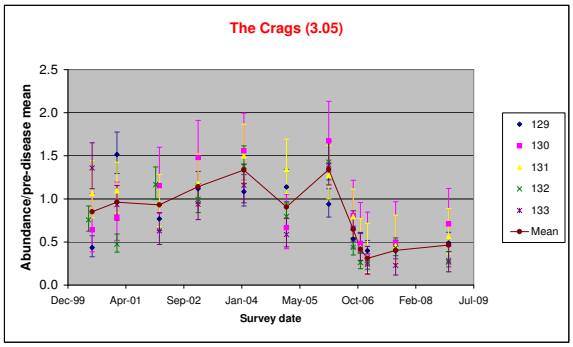
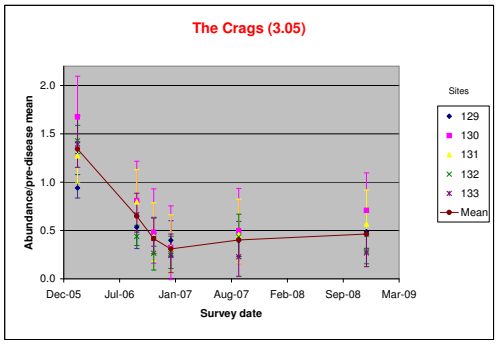


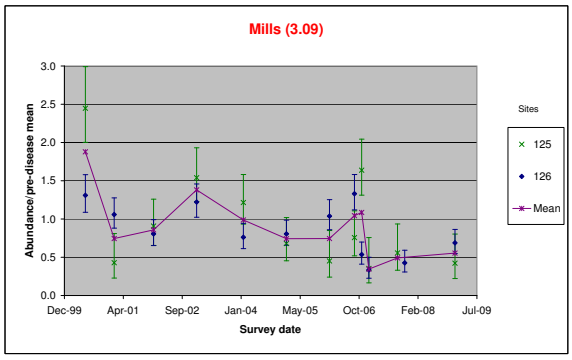
Figure 2

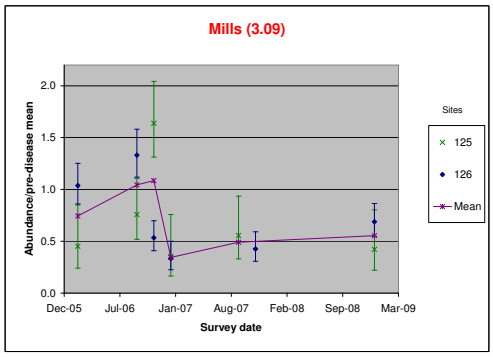

Lady Julia Percy Island (3.04)
Abundance/mean
Survey date
Dec-99
Apr-01
Sep-02
Jan-04
May-05
Oct-06
Feb-08
Jul-09
134
135
136
137
Mean

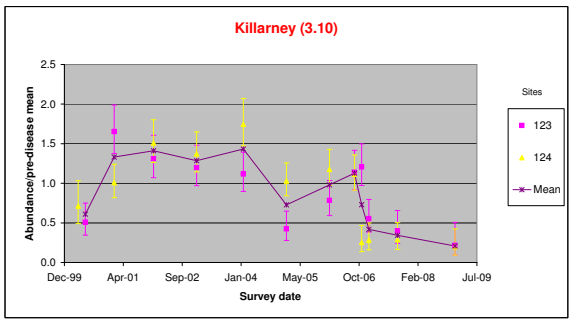

Lady Julia Percy Island (3.04)
Abundance/mean
Survey date
Dec-05
Jul-06
Jan-07
Aug-07
Feb-08
Sep-08
Mar-09
Sites
134
135
136
137
Mean

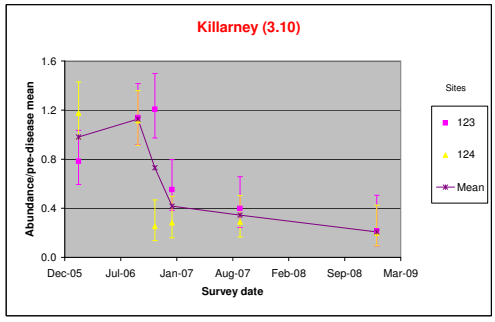

The Crags (3.05)
Abundance/pre-disease mean
Survey date
Dec-99
Apr-01
Sep-02
Jan-04
May-05
Oct-06
Feb-08
Jul-09
129
130
131
132
133
Mean

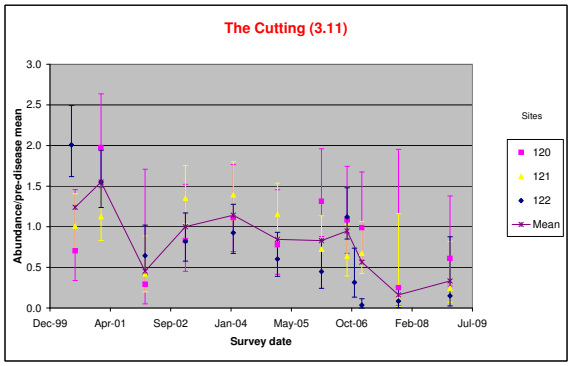

The Crags (3.05)
Abundance/pre-disease mean
Survey date
Dec-05
Jul-06
Jan-07
Aug-07
Feb-08
Sep-08
Mar-09
Sites
129
130
131
132
133
Mean


Mills (3.09)
Abundance/pre-disease mean
Survey date
Dec-99
Apr-01
Sep-02
Jan-04
May-05
Oct-06
Feb-08
Jul-09
Sites
125
126
Mean


Mills (3.09)
Abundance/pre-disease mean
Survey date
Dec-05
Jul-06
Jan-07
Aug-07
Feb-08
Sep-08
Mar-09
Sites
125
126
Mean


Killarney (3.10)
Abundance/pre-disease mean
Survey date
Dec-99
Apr-01
Sep-02
Jan-04
May-05
Oct-06
Feb-08
Jul-09
Sites
123
124
Mean


Killarney (3.10)
Abundance/pre-disease mean
Survey date
Dec-05
Jul-06
Jan-07
Aug-07
Feb-08
Sep-08
Mar-09
Sites
123
124
Mean


The Cutting (3.11)
Abundance/pre-disease mean
Survey date
Dec-99
Apr-01
Sep-02
Jan-04
May-05
Oct-06
Feb-08
Jul-09
Sites
120
121
122
Mean

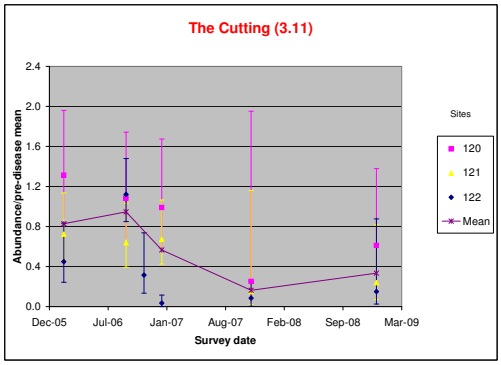

The Cutting (3.11)
Abundance/pre-disease mean
Survey date
Dec-05
Jul-06
Jan-07
Aug-07
Feb-08
Sep-08
Mar-09
Sites
120
121
122
Mean

Figure 3

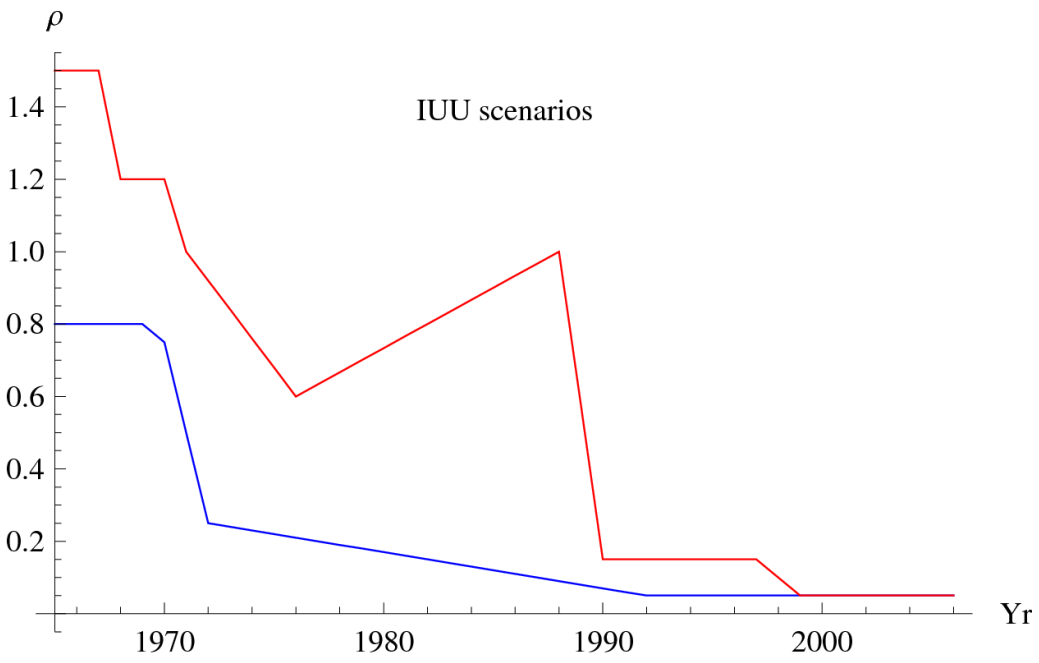
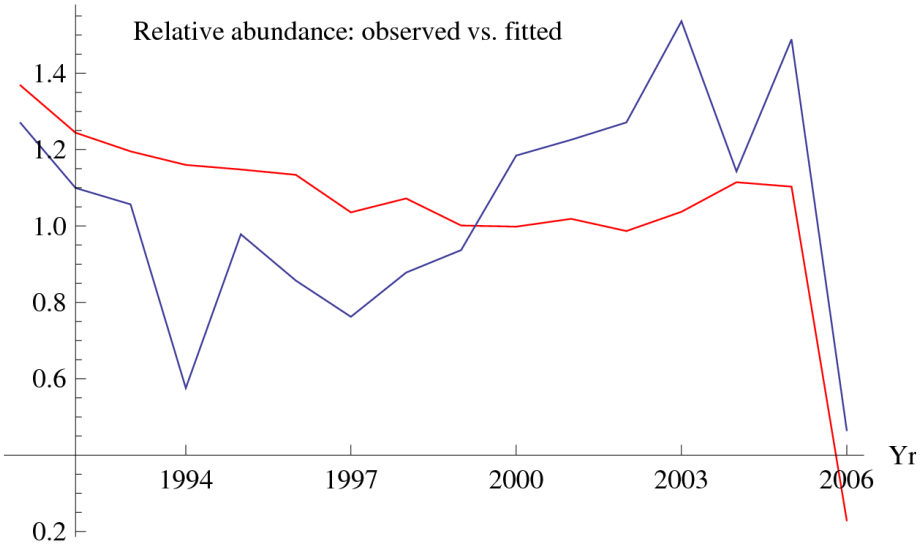


Figure 4


Relative abundance: observed vs. fitted
1.4
1.2
1.0
0.8
0.6
0.2
1994
1997
2000
2003
2006
Yr

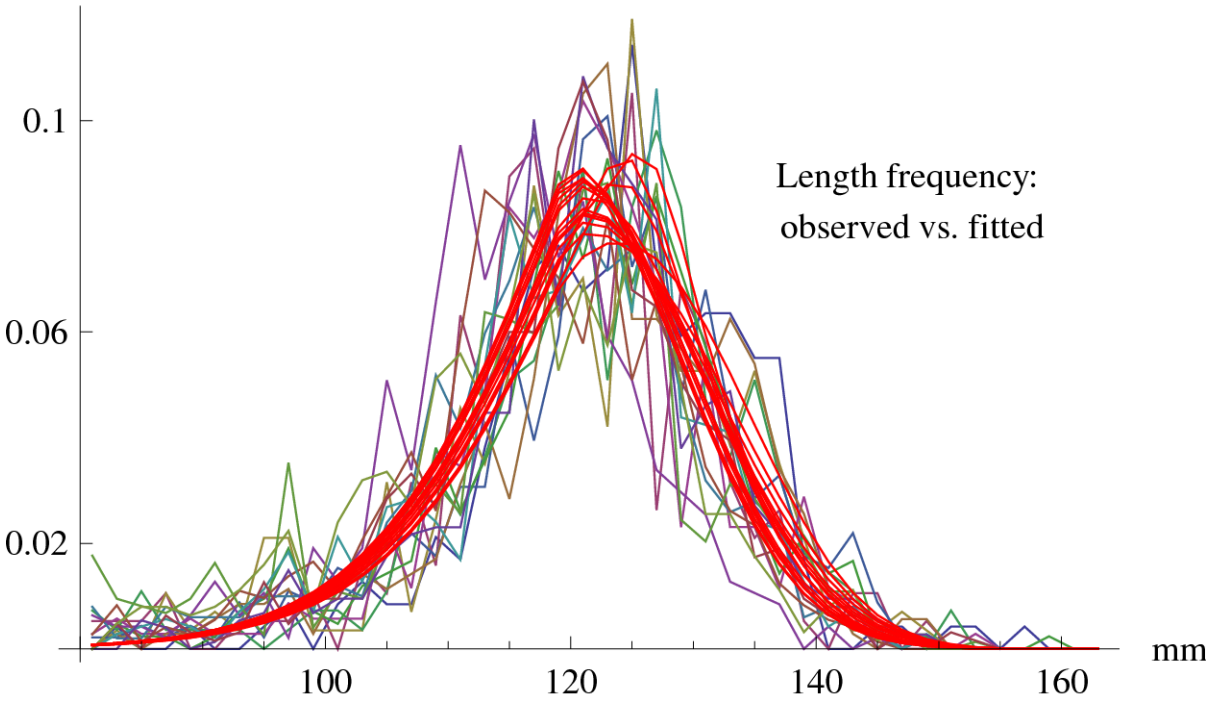

0.1
0.06
0.02
Length frequency:
observed vs. fitted
100
120
140
160
mm

Figure 5

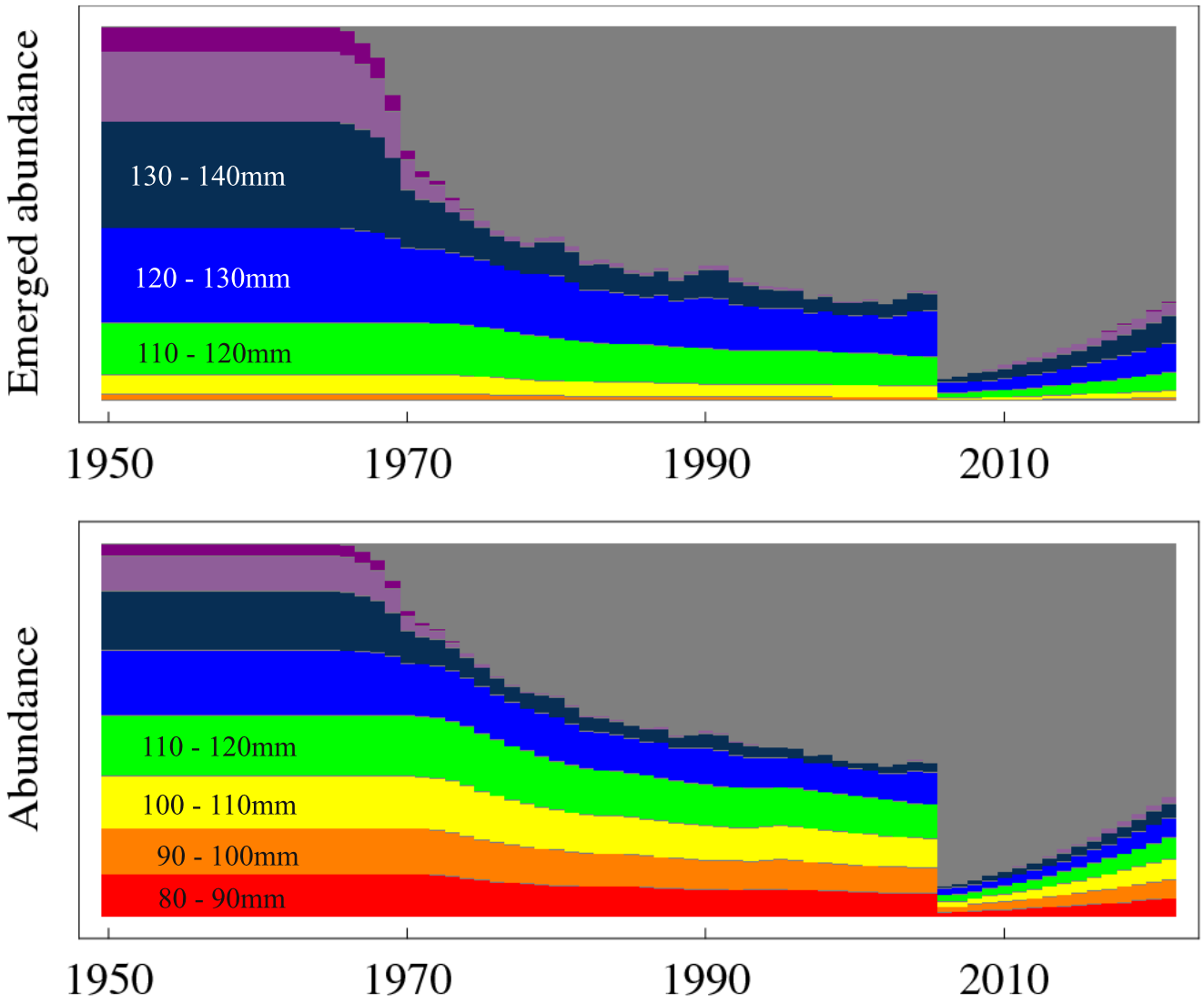

Emerged abundance
130 - 140mm
120 - 130mm
110 - 120mm
1950
1970
1990
2010
Abundance
110 - 120mm
100 - 110mm
90 - 100mm
80 - 90mm
1950
1970
1990
2010

Figure 6

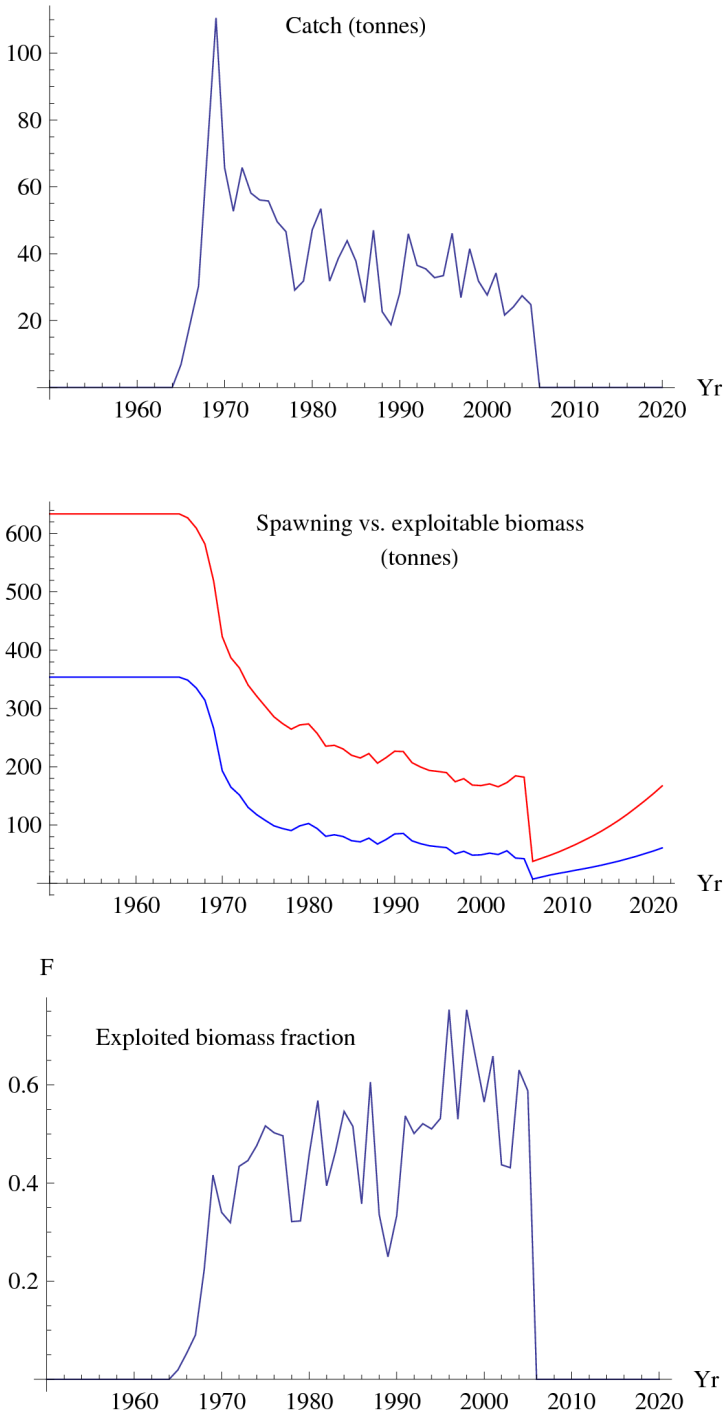

Catch (tonnes)
100
80
60
40
20
1960
1970
1980
1990
2000
2010
2020
Yr
Spawning vs. exploitable biomass
(tonnes)
600
500
400
300
200
100
1960
1970
1980
1990
2000
2010
2020
Yr
F
Exploited biomass fraction
0.6
0.4
0.2
1960
1970
1980
1990
2000
2010
2020
Yr

Figure 7

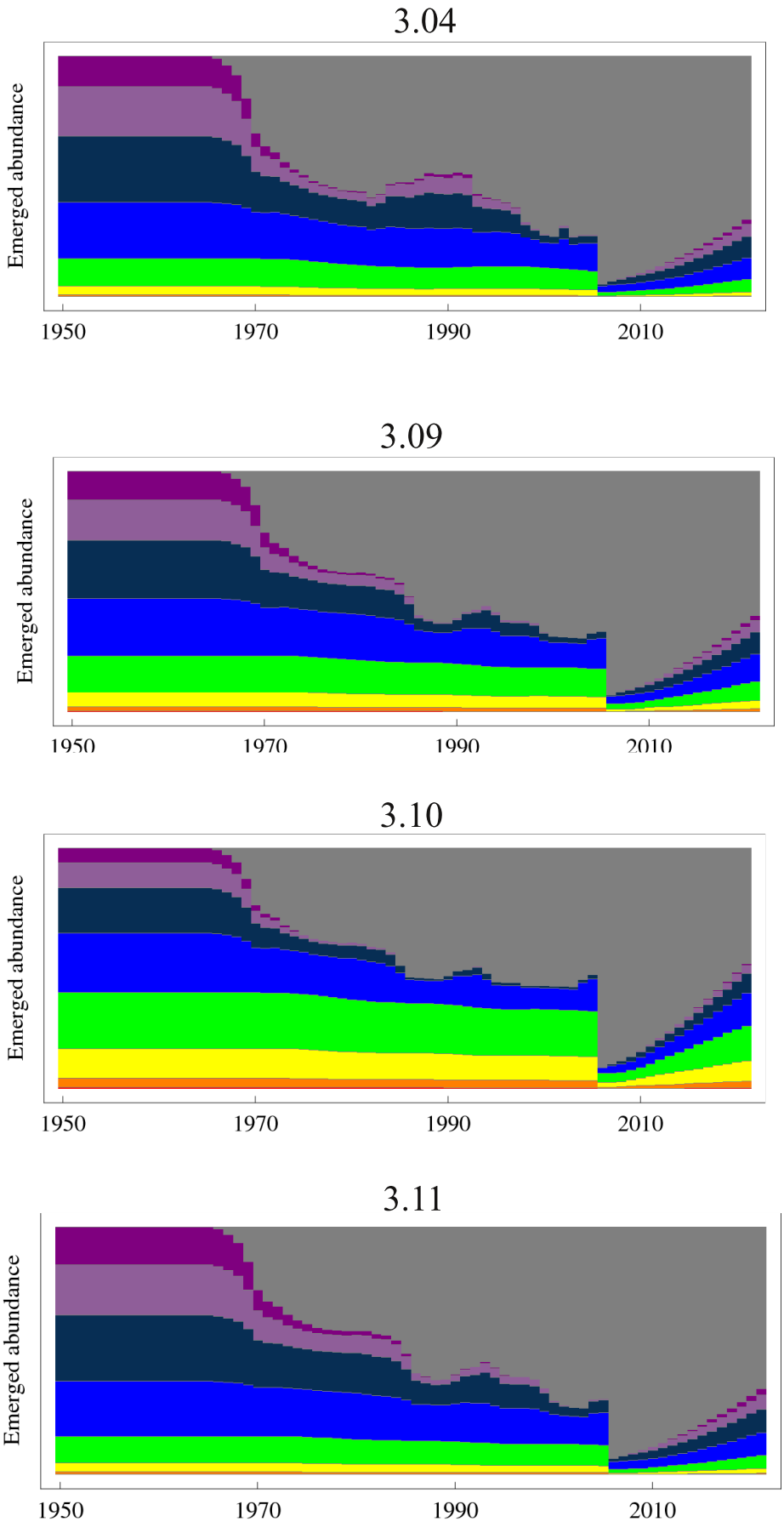

3.04
Emerged abundance
1950
1970
1990
2010
3.09
Emerged abundance
1950
1970
1990
2010
3.10
Emerged abundance
1950
1970
1990
2010
3.11
Emerged abundance
1950
1970
1990
2010

Figure 8

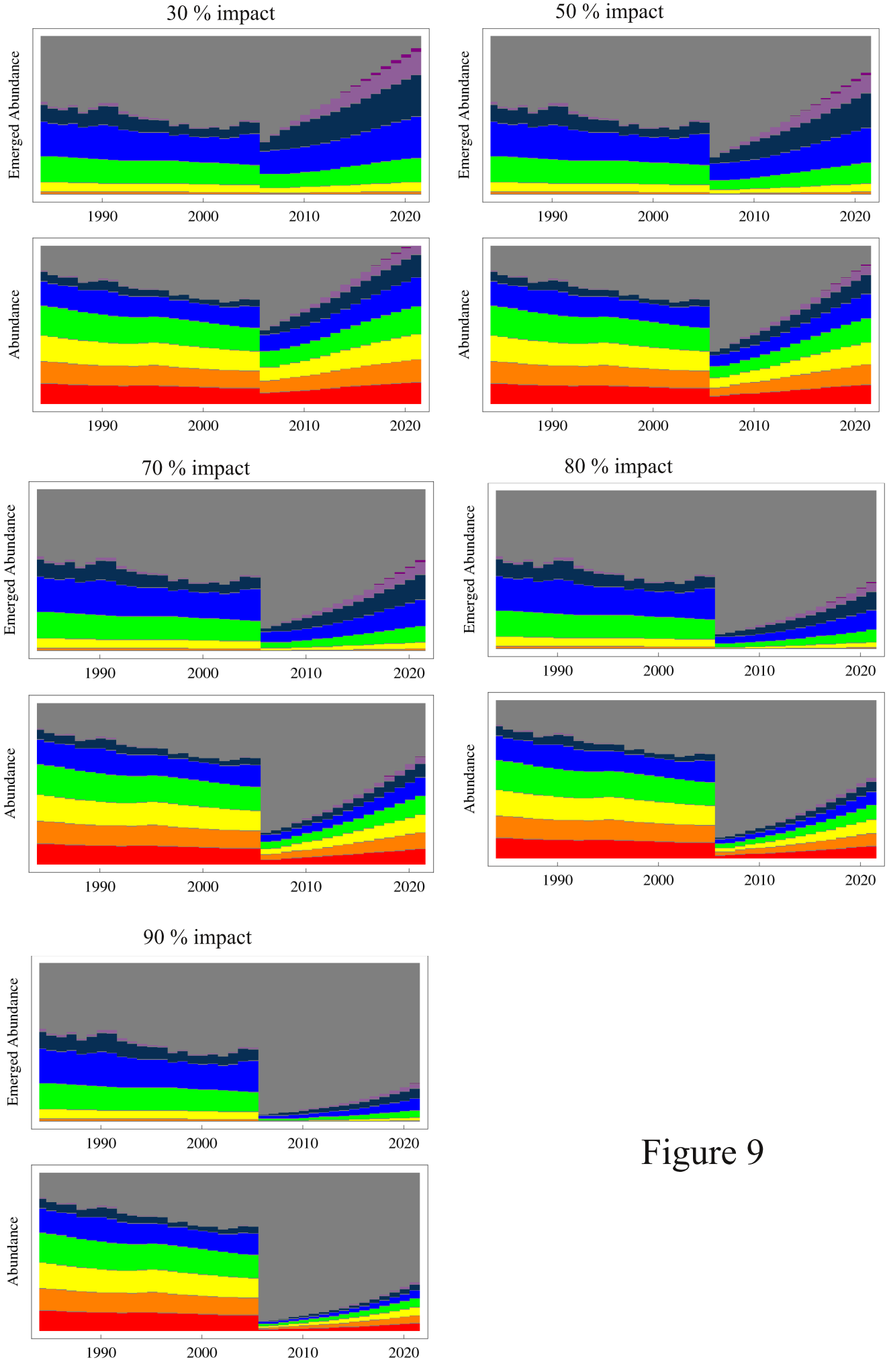
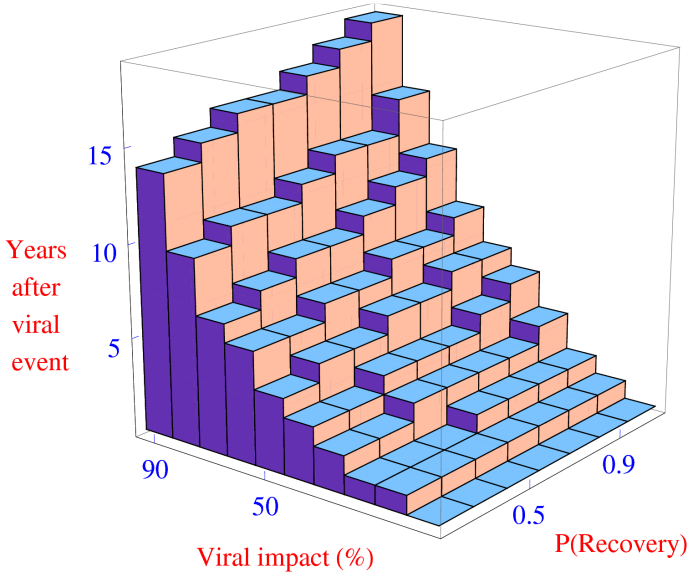
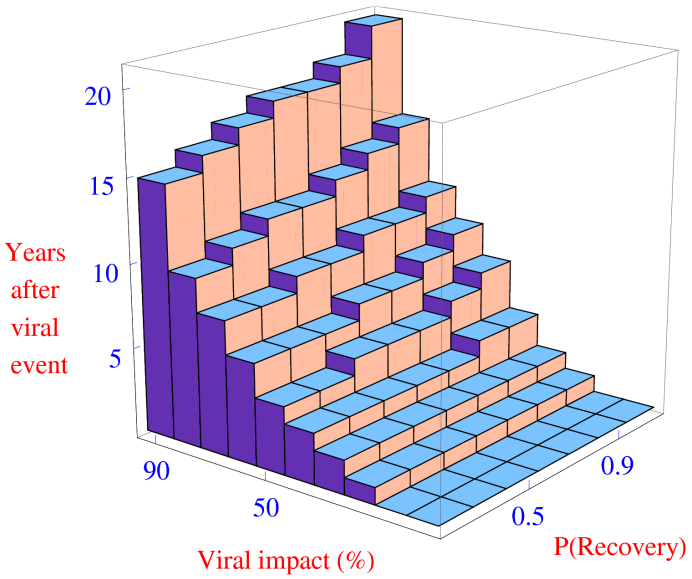

30 % impact
50 % impact
70 % impact
80 % impact
90 % impact
Emerged Abundance
Abundance
1990
2000
2010
2020

Figure 9

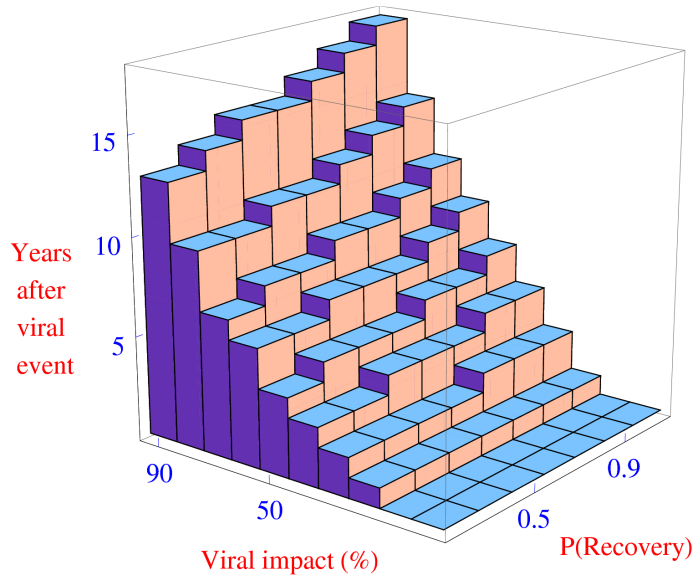
3.04



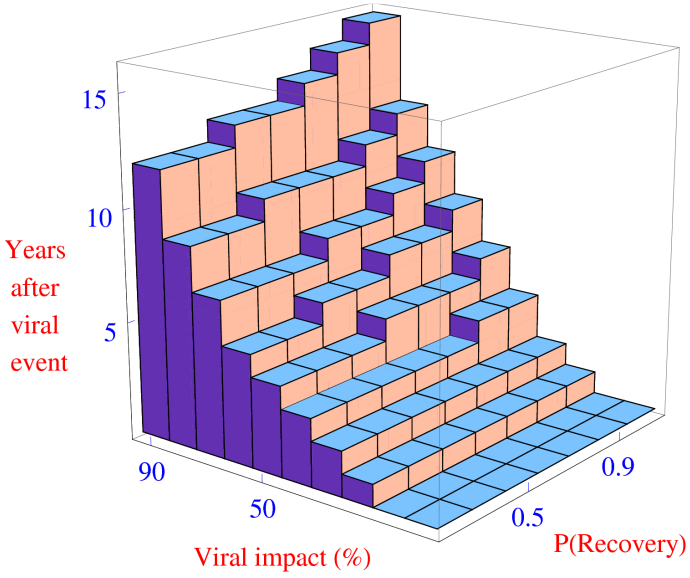
3.05



3.09



3.10



3.11

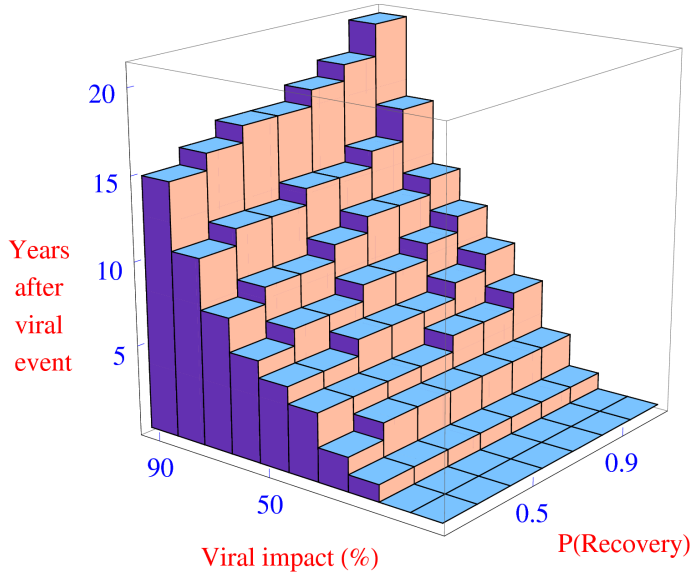
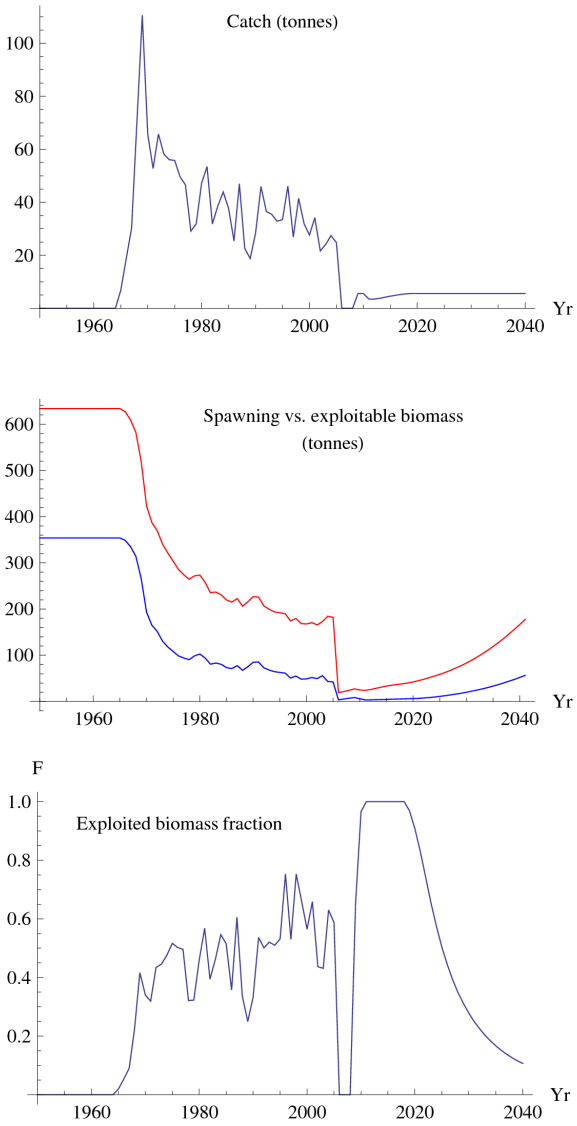


Figure 10


Catch (tonnes)
100
80
60
40
20
1960
1980
2000
2020
2040
Yr
Spawning vs. exploitable biomass
(tonnes)
600
500
400
300
200
100
1960
1980
2000
2020
2040
Yr
F
Exploited biomass fraction
1.0
0.8
0.6
0.4
0.2
1960
1980
2000
2020
2040
Yr

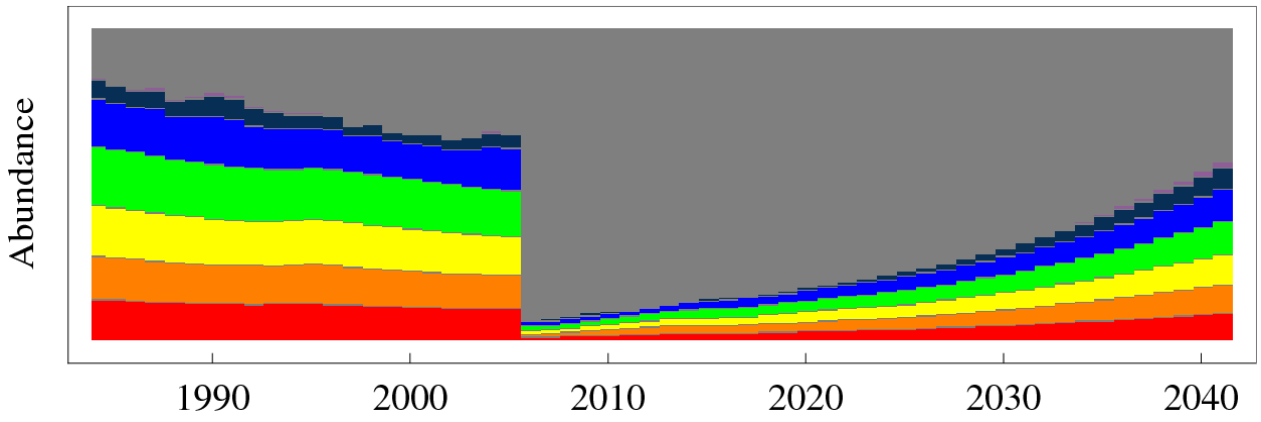

Abundance
1990
2000
2010
2020
2030
2040

Figure 11